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A CRITICAL SURVEY OF *PLANCTOMYCES* RESEARCH

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The history of the research of on *Planctomyces* genus has been summed up so as to provide a stimulus for further research.

Introduction

In Hungarian eutrophication waters including also Lake Balaton — Planctomycetes are to be found most frequently hence a survey is given of recent research results to inspire further investigations although the Hungarian researchers have done very much till now to get acquainted with the *Planctomyces* (GIMESI 1924; HORTOBÁGYI 1965, 1973, 1980; HAJDÚ 1974; OLÁH and HAJDÚ 1973).

The *Planctomyces* genus belongs to the Caulobacteriales order of bacteria. Only during the last five years some of their phyla could be isolated, so a definite dualism prevails in their taxonomy. Species have been identified on a morphological basis; there are species of biochemistry clarified from cultures, the morphological variability of which are known better. Algologists usually meet the Planctomycetes of typical form and have described many species from them. Although bacteriologists do not agree with describing the species only from their morphology, the merit of the algologist is unquestionable, without them these gemmiferous bacteria would be little known. After a long experimentation the bacteriologists succeeded in producing first an enriched culture and then a pure one. The species and morphotypes, outlined when examining the cultures, cannot be brought into perfect accordance.

Species described on morphological basis

BERGEY's Manual (1974) is used as a guide for the discussion, with our remarks where necessary.

1. *Planctomyces bekefii* (GIMESI 1924)

Synonyms: *Blastocaulis sphaerica* (HENRICI and JOHNSON 1935), *Actinothrix globulifera* (NOVÁCEK 1938), *Planctomyces subulatus* (WAWRIK 1952).

Bergey's Manual treats the *Planctomyces crassus* species (HORTOBÁGYI 1965) among the synonyms. This requires consideration. In the original description of the species is given by HORTOBÁGYI such an unusual way of propagation, by which it may be doubtful if this species belongs to the *Planctomyces* genus. According to the author the arms are pipelike and taper outwards, the gemmae form inside the pipe and stream out through the open end. Sharp-sighted algologists (UHERKOVICH 1971; HEYNIG 1979) have also found *P. crussus*, consequently the existence of the species or at least of the morphotype is confirmed. But if the same microscopic picture is interpreted as a *P. bekefii* thallus encrusted with iron so much that this incrustation covers even the older cells, then taking the *P. crassus* species as a

synonym of the *P. bekefii* may really be acceptable. The measure of inorganic iron incrustation cannot be the sole separating feature of the two species. It is uncertain, however, that dissolving the incrustation conically narrowing stipes or a usual *P. bekefii* gemma could be found, so further research is needed to elucidate this question.

The diameter of the cells is 1.4–1.7 μm, the length of the stipites is variable, the stipes is an empty pipe with fine fibres in its wall. The cells are colourless or, in large numbers, yellowish. Heterotrophic, psychotrophyl, aerobe.

2. *Planctomyces condensatus* (SKUJA 1964)

The diameter of the cells is 0.7–1.7 μm and these connect with hardly visible stipes to the central part, which can be strongly encrusted with iron. Multiplication with terminal gemmation.

3. *Planctomyces kljasmiensis* (RAZUMOV and HIRSCH 1972)

Synonyms: *Gallionella kljasmiensis* (RAZUMOV 1949), *Blastocaulis kljasmiensis* (ZAVARZIN 1961), *Gallionella planctonica* (RAZUMOV and KRASILNIKOV 1949).

Blastocaulis planctonica (RAZUMOV 1962), which has escaped the researchers' attention up to now, is also to be included in the synonyms.

The diameter of the cells is 0.3–0.5 μm or sometimes larger. The shape of the cells may alternate between roundish and longish. If the cells are longish, their longer axis is perpendicular to the stipes, i.e. they stand crosswise. They possibly multiply with gemmation.

4. *Planctomyces gracilis* (HORTOBÁGYI 1965)

The round cells are 0.3–0.6 μm in diameters, the stipes is very thin (0.3–0.4 μm) and unusually long, up to 11 μm, and is sometimes curved.

HAJDU (1976, 1977) assumed that in spite of the sharp morphological differences this species is a synonym of *P. bekefii*. This assumption is based on the analogy with the related *Caulobacter*. Namely, the *Caulobacter* increases the length of its stipes in an extremely oligotropic environment, in this way to enlarge the surface of metabolism (SCHMIDT and STANIER 1966). Not even this helps with the *Planctomyces*, that is also shown by the fact that the cells are small and almost never multiply by bipartition. Final certainty will be obtained from the investigations carried out on the *P. bekefii* cultures. The observations on the *P. maris* showed in any case that the cell size ranges from the *gracilis* size to the *bekefii* size, or even beyond that. On the basis of the variety experienced in one species conclusions can be drawn to the other species only with certain reservations, but the *P. maris* makes the existence of the *P. gracilis* as an independent species even more questionable.

With this, BERGEY's Manual closes the list of the species considered as good, but under species incertae sedis gives a list of some further discussed species.

(a) *Planctomyces ferrimorula* (WAWRIK 1956)

As it has no stipes it cannot belong to the *Planctomyces* genus.

(b) *Planctomyces guttiformis* (HORTOBÁGYI 1965)

It cannot be *Planctomyces* because of the missing stipes. It is very strange, however, to range a bacterium without stipites among those with stipites, a great many signs indicate that the *P. guttiformis* is in the right place in the *Planctomyces* genus. The intuition of an

experienced plankton researcher about the right taxonomical position seems, nevertheless, to be justified by the recent electronmicroscopic examinations (SCHMIDT and STARR 1979). In both organisms, however, features noticisible by light microscope, can be found, which point to the close relationship. Such are the small crateriform openings of the cell surface, the fine fibrils, and the threading-down daughter cells taking up an image-like position as compared to the mother cell. It can be precluded with complete certainty that *P. guttiformis* is identical with *Marssoniella* (*Gurleya marssoniella*) as it had been supposed by HIRSCH, MÜLLER and SCHLESNER (1977). Both structures are well known, their similarity is only superficial.

(c) *Planctomyces stranskae* (WAWRIK 1952)

This species, due to its incomplete and ambiguous description, had been ranged as a synonym with many other organisms. If the original description, namely that the stipites thicken towards their outer ends (just in an opposite sense as with the *P. crassus*) is accepted, but no importance is attached to it, then it belongs to the *P. bekefii*. HAJDÚ (1974) supposed that WAWRIK's datum refers really to the first presence of the *P. guttiformis* but the author misinterpreted the microscopic picture. This supposition is also reinforced by the fact that HEYNIG drew *P. guttaeformis* under the name *P. stranskae* (cf. HEYNIG 1979). On our inquiry WAWRIK insisted down to the last letter on the original diagnosis, and without type material, there is no possibility for a reexamination, either, and the remaining suspicion is not enough for the name *P. stranskae* to be considered as the right one, the *P. guttiformis* is not ranged with it as a synonym, and it cannot be recommended to do for others, either, because such a new factor, which would give reason for it cannot emerge. The bacterium identification book mentions a similarity with the *Gallionella corneola* bacterium encrusted with iron [DORFF 1934; = *Siderophaccus corneolus* (Dorff) Berger 1949]. Recently also, HORTOBÁGYI identified this species but naturally it cannot be included in BERGEY's Manual yet.

Planctomyces actinastroides (HORTOBÁGYI 1973)

The cells lie in plain, touch each other by their round ends, there is a hole in the centre of the culture, thus the culture is thimble-like. The cells gradually become thinner towards their outer ends. The gemmae are threaded down from the outer end and there they remain with a short stipes alone or by twos still for a while. Cell length is 11.7–14.3 μm, the greatest width measured at the base is 1.5–2.0 μm. The gemmae are 0.5–0.5 μm in diameter.

HORTOBÁGYI (1980) opened a new genus for the above-described *P. actinastroides* and gave it the new name: *Caulastrum danubiale* Hortobágyi. This was reasoned firstly by that the cells stood, in contrast to the *Planctomyceses* until now, not in space but in plain. The hole in the centre of the culture is also unusual. A strange contradiction is that here the stipes, connecting the gemma with the mother cell, can be found, which reinforces the Caulobacteriales relationship.

Planctomyces hajdui (HORTOBÁGYI 1980)

There are 3–5 stipites in the cultures. The stipes is thicker in the central part of the culture (incrustation? perhaps the holes formed by the basis of the stipites are wider?), becoming thinner outwards, hence its outline resembles convex or concave-sided triangle. The stipites are 6–10 μm in length, their surfaces are smooth. The cells are 0.6–1.0 μm in diameter. The spores, similarly to those of the *P. crassus*, swarm out of the inside of the stipites.

According to the logic of BERGEY's Manual this species is also the synonym of the *P. bekefii*, but a final answer can be given only after the culture experiments are cleared up its natural variability, or if *P. bekefii* can be produced by hydrochloric iron dissolution from the individuals of *P. hajdui* collected from nature.

Species described from cultures

Only one species is known, which has been described according to the bacteriological rules; it is the *Planctomyces maris* (BAULD and STALEY 1976). The diameter of the cells ranging from roundish to oviform is 0.4–1.5 μm. Attention must be paid to the fact that the variability of the cell size includes not only the *P. bekefii* but also the *P. gracilis*. The stipes of filose structure is 5 μm in length, its diameter is 0.05–0.10 μm. The gemmae are threaded down at the cell ends opposite to the stipes. The daughter cells move with flagella, the flagellum can be found near the origin of the stipes, this can sometimes be seen in the cells of the developed culture. Gram negative. It is isolated from the sea, and needs Na^+ ion in at least 100 mM NaCl quantity. A conciderable increase of the cells can be observed only with a salinity of 1.5–4 weight volume per cent. Heterotrophic, obligate aerobe, mesophilous: heat optimum is 30–33°C, above 37.5°C and under 6°C there is no growth. The isolated population was placed in the international culture collection as it is required by the bacteriological rules.

Following this track, SCHMIDT (1978) isolated *Planctomyces* populations from fresh water, too, and making thereby a considerable contribution. In the very article he gives an account of the fresh water *Planctomyces* populations isolated in the GFR, too. The most surprising fact is that there is much greater morphological variability in the enriching and pure cultures than in the samples collected in nature. The populations are obligate aerobes, they grow best at 25–30 °C. Even 50 mM NaCl impeded their growth, thus they are sharply delineated from the *P. maris*, biochemically. Moving with a flagellum can also be observed here. Autolysis can often be seen when the cells are grown in glucose supply solution or without bivalent cations. 5–10 mM $MgSO_4$ or $CaCl_2$ is already enough to stabilize the cell membrane. Incidental note: *Planctomyceses* can be frequently found in the waters of high calcium contents in Hungary, too. They are resistant to penicillin in a quantity of 5000 μ/ml and to the d-cycloserin in a quantity of 0.1 mg/ml.

Electronmicroscopic morphology of the cultivated

Planctomyceses

Here a summary of the observations made known in separate papers will be attempted. SCHMIDT's (1978) detailed examinations have extended our knowledge about the electromicroscopic ultrastructure of the *Planctomyces bekefii*. An electromicroscope of larger resolving power was available for him which was not for the earlier researchers (KALBE, KEIL and THEILE 1965; OLÁH and HAJDU 1973), so he could clearly observe some finer details, too. He described, for example, that the thickness of the elementary fibrils of the stipes is 3–4 μm. He described the flagellum starting from the vicinity of the origin of the stipes. The flagellum can extend from one-third of the stipes length to a multiple stipes length, its thickness is below that of the stipes. The cells range between 0.8–2.5 μm in diameter. As the cells have no rigid cell walls, their size also depends on the osmotic pressure. Attention must be paid

to the fact that a cell diameter, larger almost by 1 μm, in the cultures than that to be found in nature, was measured. Such a big cell, as well as the great many morphological features (appendage, stipes, cell polarity, etc.) are surprising in a bacterium. In a thin supply-solution which is similar to that of the conditions of the original habitat, multiplication takes place by germination but in a thicker supply-solution (the common quantity of the yeast extract and peptone was raised from 0.001–0.01% to 0.1%) a multiplication by bipartition takes place and the characteristic stipes forms neither. The question emerges if the *Planctomyces* had already been isolated earlier, was it only that its belonging to the gemminating bacteria with stipites was not recognised in the thick supply solution.

SCHMIDT and STARR (1978, 1979, 1980) devoted separate articles to the morphological characterization of several populations. Unfortunately, the morphotypes found can be brought into coincidence only approximately with the species known up to now. In the cultures such a stipe-type could also be found where the elementary fibrils stand thicker than usual and the stipes are often twisted, which renders the whole stipe ropelike. Its taxonomical value is questionable, because BAULD and STALEY mention when describing the *P. maris* that there is a possibility for such morphotypes to form. It can be supposed that the ropelike stipes belong to the natural variability of *P. bekefii*. The stipes can be described as tubular because it becomes flat and ropelike only on the electronmicroscopic mount. Definite efforts are made by the authors to give a separate name to each formula, creating thereby, in our opinion unnecessary terms as for example, the spire. This appendage derives, similarly to the fine fibrils the fimbriae, from the cells but is thicker than those, differs from them by its more rigid character and a fibriform structure similar to the stipe can be observed more finely but definitely. Studying a sample collected in nature under the light microscope, it immediately becomes obvious that there is no question of an accidental coincidence, there are also stipites and it is unnecessary to give them new names. The gemmae do not sometimes come off the mother cell but shoot from a stipe there, and thus arises the compound culture thallus to be observed so frequently in natural materials. During the preparation for the electronmicroscopy the daughter cells fall off, burst into pieces, and only the empty stipites can be seen branching out of the mother cells.

Some more words about SCHMIDT and STARR's (1979) article written on the *P. guttiformis*. There is a serious mistake in the referred work. Reading HAJDÚ's article (1974) they skip over a note at the top of p. 179, namely that the thorn and the other observed new features could be observed in the original type material, too. There are no doubts that the original HORTOBÁGYI's *P. guttaeformis* and the *P. guttaeformis* studied under the light microscope are identical. This instigated HAJDÚ to give a new diagnosis at that time (p. 180). Instead of the name *P. guttiformis* Hortobágyi (sensu HORTOBÁGYI) the right author name is *P. guttiformis* Hortobágyi emend. Hajdú. SCHMIDT and STARR reinforce HAJDÚ's earlier electronmicroscopic observations to the smallest detail, moreover, in some details, requiring finer analysis, they offer something that is new. It is surprising that they did not discover the unit membrane structure in the cellular membrane, moreover the structure differs totally from that usual with the *Grambacteria*. It cannot be understood, however, why the denomination "spine" is better than "spike" for the cell appendage. The same applies to the cell form. The word "bulbiform" recommended by the authors is not much better than the word "pear-shaped" used by HAJDÚ, since the resemblance depends on the bulb or pear species, one thinks of. In any case we cannot agree with the authors' effort to introduce a great many new morphological terms, which are, in most cases, unnecessary.

Discussion

Isolation has to be one of the first conditions for developing the investigations in Hungary. If the water sample taken from nature is to be enriched for *Planctomyces*, then it has to be aired thoroughly (because it is aerobe); it is to be kept in the dark (because it does not require light while darkness forces the competing algae back); add to it 0.04 peptine and 0.02% yeast-extract (because it is heterotrophic); if the quantity of the bivalent cations does not reach 5–10 mM, then it is to be completed to this quantity (the cell membranes are stabilized); penicillin or other antibiotics have to be added to the culture (it does not cause damage to the *Planctomyces* but restrains other heterotrophic bacteria multiplying much more quickly), enrichment takes a long time, they multiply very slowly, furthermore many of them adhere to the wall of the glass and these can hardly be extracted), the water samples are to be kept at 25–30 °C (mesophilous).

Planctomyces is a real saprobity indicator. The saprobe system is mostly built on anaerobia-resistant organisms, although conclusions can be drawn from there as to the organic-matter content. The *Planctomyces bekefii* lives rather in betamesosaprobe waters than in alphamesosprobe ones.

The question, if the daughter cells come off the *P. guttiformis* directly or by the interposition of the stipes, has not been cleared up yet. But it is obvious, however, how the daughter cells with their stipites penetrate the centre of the thallus. As first the thallus is only of four rays and the number of the rays can amount to fifty in extreme cases. From the point of view of fluid mechanics the task is impossible to be solved with a flagellum which starts from the base of the stipes. It is obvious that the stipes has to point ahead when swimming towards the thallus centre and, in this case, the flagellum can be nothing but a pull flagellum. With a flagellum not being inserted in an axis, however, it is hardly possible to swim straight. This point requires further examination.

What can the explanation be for this peculiar thallus-structure? Of course, here one can rely only on speculations, or an analogy with other water microorganisms. If this peculiarity has been kept, then, it has to mean an advantage to the *Planctomyces* from some point of view or other. The cells at the ends of the stipites standing in radial direction need not udeup the organic matter from each other in the otherwise oligotrophic water and this is an advantage not to be neglected. It is, however, much more important from the point of view of the *Planctomyces* that it cannot be swallowed due to the large thallus by the planktons, so the grazing loss is small. A bacterium, whose multiplication is slow like that of *Planctomyces*, could not constitute a considerable population, if it did not protect effectively against grazing. By means of their flagella the torn off cells can look for the detritus granules and consume algae and the released organic matter.

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CONTRIBUTION A L'ÉTUDE DU GENRE DIPLASIOLEJEUNEA (SPRUCE) SCHIFFNER, 4.

LA SECTION *VILLAUMEAE* P. TX. (SUBGENUS *DIPLASIOLEJEUNEA*) SUR LA COTE EST DE MADAGASCAR

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A regional monograph of the section *Villaumeae* Tixier with eight species: *D. ensifera*, *D. insignis*, *D. jonesii* sp. n., *D. lemuriana*, *D. palustrium* sp. n., *D. phyllarthronii* sp. n., *D. tridentata*, *D. villaumei*.

L'auteur poursuit l'étude des Lejeuneacées sur la côte Est de Madagascar. En ce qui concerne la description de la végétation malgache, il renvoie à l'œuvre magistrale de PERRIER de la BATHIE (1921).

L'auteur a décrit, dans le sous-genre *Diplasiolejeunea* (SCHUSTER 1970), la section *Villaumeae* (TIXIER 1977), définie par ses grandes feuilles (tiges larges avec les feuilles de 2.3 mm), ses ocelles petites et dispersées, ses feuilles à lobe obtus et lobule large, les amphigastres bifides à lobe également obtus.

Enfin, en 1980, il a signalé la répartition biogéographique des sections *Diplasiolejeunea* et *Villaumeae* en Afrique et an Amérique tropicales. La première de ces sections demeure essentialement caraïbe et sud-américaine avec une seule espèce africaine, *D. albifolia* (Tayl.) E. W. Jones répartie entre Nigérie et Tanzanie.

En opposition la section *Villaumeae* est essentiellement africaine et malgache (elle ne semble pas signalé dans les archipels des Comores, des Seychelles et des Mascareignes). On la rencontre en Amérique, de façon moins répandue et comprenant un certain nombre d'espèces: *D. unidentata* (Lehm. et Lindenb.) Schiffn., *D. heimii* Jovet-Ast, *D. johnsonii* Evans et *D. pauckertii* (Nees) Steph.

La première liste d'espèce, liste exhaustive du genre *Diplasiolejeunea*, est dues à STEPHANI (1916). Dans la section que nous envisageons et pour l'Afrique, les espèces se réduisent à *D. runssorensis* Steph. et à *D. villaumei* Steph. La première espèce provient d'une récolte de STUHLMANN, en 1891; un autre échantillon d'origine malgache est du à Forsyth Major. La seconde espèce a été trouvée par le R. P. VILLAUME, entre Tananarive et Antevorante (sur la côte) et probablement entre les localités d'Angavokely et d'Analamazotroa.

En 1965, VANDEN BERGHEN a redrécrit *D. runssorensis* et le signale au Kivu, vers 3 000 m, au Mont Lugoma, et, au Rouanda, à 1 950 m, vers Shangugu.

E. W. JONES (1975) ajoute à l'espèce *D. runssorensis*, la variété *australis* à partir de l'échantillon Forsyth Major (G-506). Il retrouve cette variété en Tanzanie, dans les montagnes du Sud et dans la région de l'Usambara, entre 860 et 1 750 m. Ces récoltes ont été faites en compagnie de T. PÓCS. JONES ne semble pas avoir examiné *D. villaumei*. PÓCS (1974), de son côté, signale *D. runssorensis* en Tanzanie, vers 1 700–1 800 m. Il a eu l'obligeance de nous prêter un certain nombre d'échantillons. Parmi ceux-ci, R. GROLLE a indiqué une forme *depauperata* (in sched.).

Les récoltes analysées ici s'étagent du lac Alaotra au nord de la ville de Fianarantsoa, à des altitudes s'échelonnant de 900 m à 1 800 m, avec une préférence pour les stations situées entre 1 200 et 1 400 m.

La répartition de ces taxons, à affinités corticoles plutôt qu'épiphylles rest. liée à deux facteurs qui ne sont pas toujours liés, à savoir une climatologie d'altitude et la présence d'un certain type de formation forestière.

Rappelons que Madagascar possède un relief dissymétrique, l'île étant large de 500 à 600 km, la dorsale orientale se trouve à moins de 200 km de la côte Est.

Le relief est constitué d'Est en Ouest, à partir de la plaine côtière en premier lieu de la falaise betsimisaraka, suivie de la plaine de l'Ankay, vers 1 000 m, dominée par la dorsale de l'Angavo, qui atteint 1 200 m, elle débute un peu au Nord du lac Alaotra et finit vers le massif de l'Andringitra, au Sud de Fianarantsoa. En arrière de la crête de l'Angavo, le relief demeure plus confus. Dans le Nord, à la hauteur de Tananarive, de petits dômes granitiques isolés se succèdent, à partir du Nord d'Anjozorobé, le plus célèbre restent Angavokely, résidu forestier, site plus ou moins religieux et transformé, assez tôt, en station forestière. D'autres petits massifs sembables ont existé ou subsistent à un état très dégradé. Tananarive s'est appelé à l'origine Analamanga (la forêt bleue). Ambohimanga et Andramasina possèdent encore des lambeaux forestiers très dégradés par le ramassage du bois mort et le paturâge sous forêt.

Plus au Sud, entre Tananarive et Antsirabé, se dresse le massif volcanique de l'Ankaratra (2 600 m). Ce massif, comme le massif de l'Andringitra possède la particularité d'avoir des forêts denses « suspendues », réfugiées dans des vallées assez larges qui rappellent les sholas du Sud de l'Inde (Blasco 1971).

La formation préférée des taxons de la section *Villaumeae* est constituée par les formations de passage entre la forêt dense d'altitude (à un seul étage d'arbre et la brande à *Philippia*). Cette dernière formation ressemble à la lande européenne à bruyères. C'est en plus une formation « bouche-trou ». Elle couronne, en principe, les crêtes où elle atteint 50 cm de haut, atteignant 4–5 m en bordure des forêts vallicoles dense dans les vallées de la région du Haut Mangoro.

Clé des espèces de la section pour Madagascar

1 Apex du lobule à trois dents ..... 1 *D. tridentata*
1' Apex du lobule à deux dents
  2 Dent médiane genouillée ..... 2 *D. insignis*
  2' Dent médiane droite 3

3 Lobule longuement décurrent
  4 Dent médiane à 2 rangs de cellules jusqu'au sommet 3 *D. lemuriana*
  4' Dent médiane à plusieurs étages monocellulaires .....
  vers l'apex ..... 4 *D. ensifera*

3' Lobule peu décurrent
  5 Dent médiane double
    6 Dent médiane longue ..... 5 *D. phyllarthronii*
    6' Dent médiane courte ..... 6 *D. palustrium*
  5' Dent médiane simple
    7 Dent médiane longue ..... 7 *D. villaumei*
    7' Dent médiane courte 8 *D. jonesii*

1. Diplasiolejeunea tridentata P. Tx. (Fig. 1)

Rev. Bryol. Lichénol. 45,2: 223, 1979.
ICONES: TIXIER, Rev. Bryol. Lichénol. 45,2: 224, fig. 8, 1979.

Plante moyenne, vert-jaune, corticole. Tiges atteignant 1 cm, épaisses de 60 μm, larges avec les feuilles de 1,8 mm. Feuilles insérées sous un angle de 90° et distantes entre elles de 0,4 mm. Cellules marginales à parois minces, carrées, de 20 × 20 μm, cellules basales à parois épaissies et à trigones, hexagonales de 30–70 × 15–25 μm. Ocelles peu nombreux. Lobe oval avec une carène peu arquée, recouvrant la tige, long de 1,20 mm, large de 0,9 mm. Lobule en sac, enflé, avec une marge supérieure recurvée, largement tronquée au sommet. Dent apicale

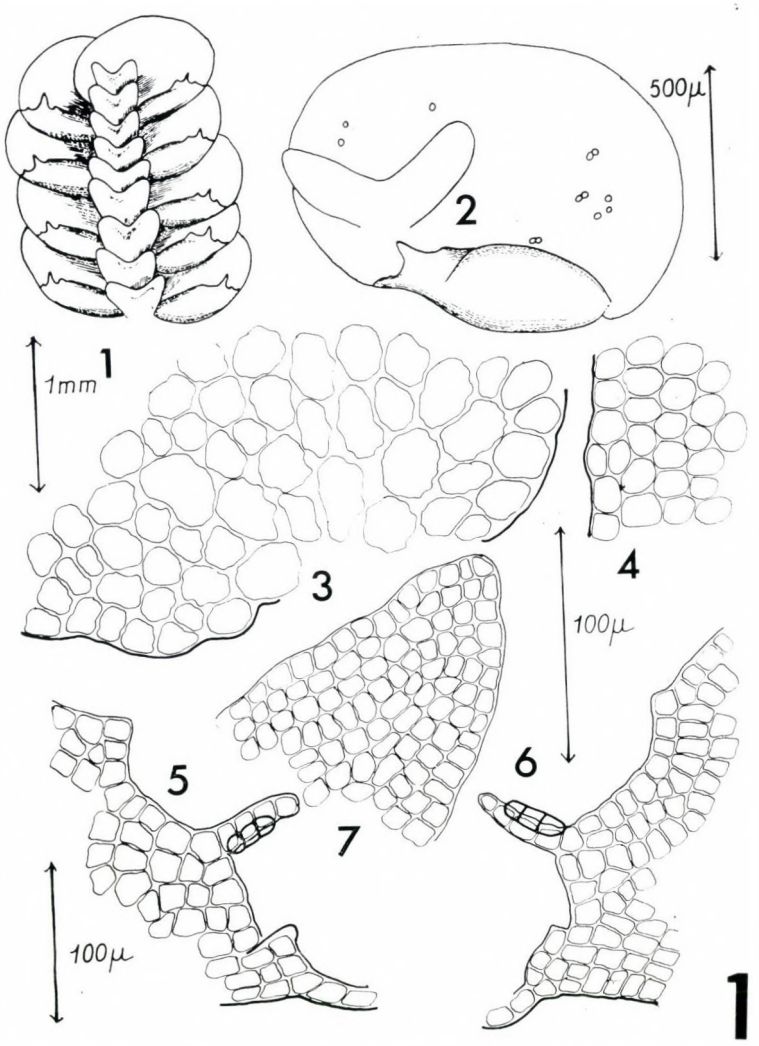


Fig. 1. — Diplasiolejeunea tridentata P. Tx. (holotype)
1: tige, 2: feuilles et amphigastres, 3: base du lobe, 5–6: apex du lobule, 7: demi-amphigastre

petite, dent médiane avec deux étages de cellules, dent submédiane à proximité de la carène. Amphigastres en forme de V, hauts de 0,3 mm, larges de 0,6 mm, avec des lobes arrondis au sommet. Propagules discoïdes, de 150 μm de diamètre et à 46 cellules. Epi mâle latéral haut de 1 mm et à 3 étages de bractées fertiles. Plante probablement dioïque.

Echantillons examinés: Tamatave, Manoitaly (Route du Chrome), 1 200 m, forêt de crête, 19. 4. 1978, TIXIER 11763 — Moramanga, route d'Anosibé-Anala, 1 100 m, 18. 4. 1978, TIXIER 11699 — Route de Lakato, 1 000 m, forêt dense vallicole, 2. 6. 1979, TIXIER 12591 — Fianarantsoa, forêt près d'Ambatofitorahana, 1 650 m, corticole en forêt, 29. 12. 1976, TIXIER 10140 (holotype in coll. auct.).

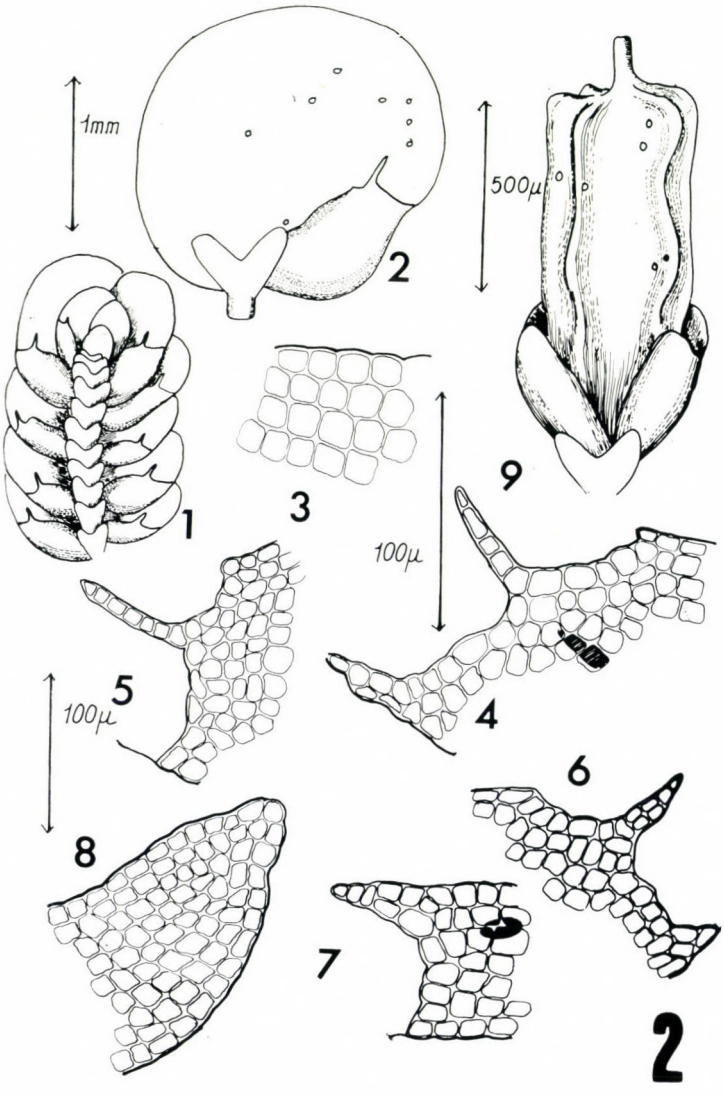


Fig. 2. — Diplasiolejeunea insignis P. Tx. (holotype)
1: tige, 2: feuille, 3: feuille à propagules, 4: apex du lobe, 5: base du lobe, 6: apex du lobule des feuilles, 7: apex du lobule des feuilles à propagules, 8: amphigastre, 9: propagule

2. Diplasiolejeunea insignis P. Tx. (Fig. 2)

Lindbergia, 4, 1–2: 120, 1977 & Nova Hedwigia, 34: 751, 1980.
ICONES: Tixier, Lindbergia, 4, 1–2: 119, fig. 2, A–I, 1977.

Plante petite, vert-bronze, corticole. Tiges longues jusqu'à 1 cm, épaisses de 100 μm, larges avec les feuilles de 1,4 mm. Tige, en section, avec trois cellules médullaires et sept corticoles. Feuilles insérées sous un angle de 90° et distantes entre elles de 0,3 mm. Cellules à parois minces non ornées. Vitta composée d'une dizaine d'ocelles fugaces de 15×25 μm. Cellules marginales isodiamètriques de 15 μm de diamètre, cellules basales de $20–25 \times 15–20$ μm. Feuilles caulinaires à lobe oval-arrondi, sans sinus entre le bord de la feuille et la carène du lobule, couvrant légèrement la tige, long de 0,6 mm, large de 0,5 mm. Lobule grand (2/3 de la feuille), en sac, gonflé, long de 0,4 mm, large de 0,15 mm, à apex tronqué, dent apicale plus ou moins en crochet, dent médiane genouillée à 3 cellules. Papille hyaline sous le lobule, ovale et longue de 20 μm. Feuilles propagulifères plus grandes, ovales, allongées, longues de 1,7 mm, larges de 0,7 mm. Bords de la feuille recurvés vers l'extérieur. Lobule allongé, dents à l'apex peu visibles. Amphigastres à lobes divergents et larges, hauts de 0,43 mm et larges de 0,3 mm. Propagules discoïdes de 100 μm de diamètre à 34–43 cellules. Plante dioïque. Périanthe observé à l'état juvénile. Epi mâle à 5 étages de bractées fertiles.

Echantillons examinés: Tananarive, Angavokely, 1 800 m, corticole en brousse d'altitude, 23. 6. 1976, Tixier 8731, 8744 — idem, 27. 1. 1977, Tixier 10258 (Holotype, PC), 10259, 10260, 10261 — idem, 20. 5. 1977, Tixier 10438, 10439, 10440, 10441, 10442 — idem, 12. 9. 1977, Tixier 10788, 10789, 10790, 10792 — Tananarive, Angavobé, 1 600 m, 15. 9. 1977, Tixier 10820, 10821, 10822, 10823, 10828, 10829, 10830 — Tananarive, Andavotoatomaizina, 1 500 m, 14. 1. 1978, 11022, — idem 21. 1. 1978, Tixier 11039, 11040, 11042, 11043, 11046, 11047, 11048, 11059.

3. Diplasiolejeunea lemuriana P. Tx. (Fig. 3)

Lindbergia, 4, 1–2: 120, 1977.
ICONES: Tixier, Lindbergia, 4, 1–2: 121, fig. 3, A–I, 1977.

Plante grande, vert jaunâtre, corticole. Tige jusqu'à 1 cm, peu ramifiée, épaisse de 0,10 mm, large avec les feuilles de 2 mm. Tige en coupe avec 6 cellules médullaires et 8 cellules corticoles, cependant la coupe étant faite à l'insertion de la feuille et de l'amphigastre, on peut supposer qu'il y a eu augmentation du nombre des cellules des deux sortes. Feuilles insérées sous un angle de 90° et distantes entre elles de 0,3 mm. Cellules marginales carrées de 16×15 μm, cellules basales avec quelques petits épaississements intermédiaires $15–30 \times 15–20$ μm. Quelques ocelles sur la feuille et le périanthe. Lobe oboval couvrant à peine la tige, long de 1,3 mm, large de 0,9 mm. Lobule très long inséré sur le bord récurvé de la feuille, long de 0,8 mm, large de 0,2 mm. Bord supérieur du lobule récurvé jusqu'à la dent apicale. Dent apicale peu marquée, dent médiane en T, comme chez *D. javanica* mais plus large et plus haute. Papille hyaline sous la base de la dent médiane, obovale longue de 30 μm. Amphigastres largement divisés, à lobes divergents arrondis au sommet, hauts de 0,3 mm, larges de 0,5 mm. Plante dioïque (?). Inflorescence femelle à une innovation latérale. Bractéole arrondie, bifide au sommet. Bractées périanthaires courtes à lobe et lobule égaux, longs de 0,4 mm, larges de 0,2 mm. Périanthe haut de 1,3 mm, large de 0,5 mm, cylindrique à 4 plis. Bec peu marqué.

Echantillons examinés: Tananarive, Ambatoloana, forêt d'Ankéramitra, 1 200 m, 10. 11. 1976, Tixier 9636 — idem, Andasibé, 1 200 m, brousses secondaires en bordure de prairie marécageuse, 10. 11. 1976, Tixier 9624 — idem, Manjakandriana, Lac Mantasoa, villa Danièle, brousse éricoïde, 1 400 m, 19. 4. 1976, Tixier 8159 — idem, La Mandraka; 1 200 m, 22. 9. 1977, Tixier 10935 — Tamatave, Anālamazotra, 850 m, 5. 7. 1977, Tixier 10620 — Fianarantsoa, Vohiparara, brousse éricoïde, 1 200 m, 30. 12. 1976, Tixier 10171 (Holotype, PC).

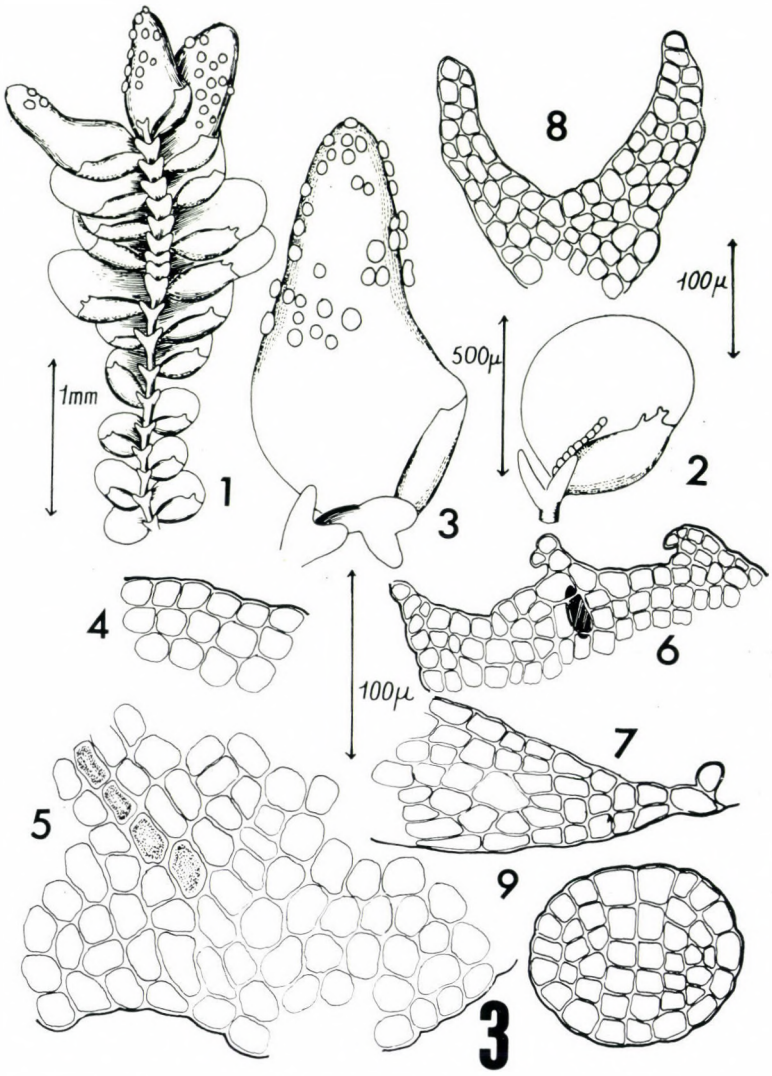


Fig. 3. — Diplasiolejeunea lemuriana P. Tx. (holotype)
1: tige, 2: feuille et amphigastre, 3: base du lobe, 4: sommet du lobe, 5–6: sommet du lobule, 7: demi-amphigastre, 8: périanthe

4. Diplasiolejeunea ensifera P. Tx. (Fig. 4)

Rev. Bryol. Lichénol. 54,4: 215–217, 1979.
ICONES: Tixier, Rev. Bryol. Lichénol. 45,4: 216, fig. 4, 1–9, 1979.

Plante moyenne, vert jaunâtre, corticole sur les branchettes. Tiges longues jusqu'à 1 cm, de 50 μm de diamètre, larges avec les feuilles de 1,5 mm. Feuilles insérées sous un angle de 90° et distantes entre elles de 0,3 mm. Cellules foliaires à parois minces, cellules marginales de 15 × 15 μm. Peu d'ocelles sur le lobe et le périanthe. Lobe couvrant la tige, arrondi, carène

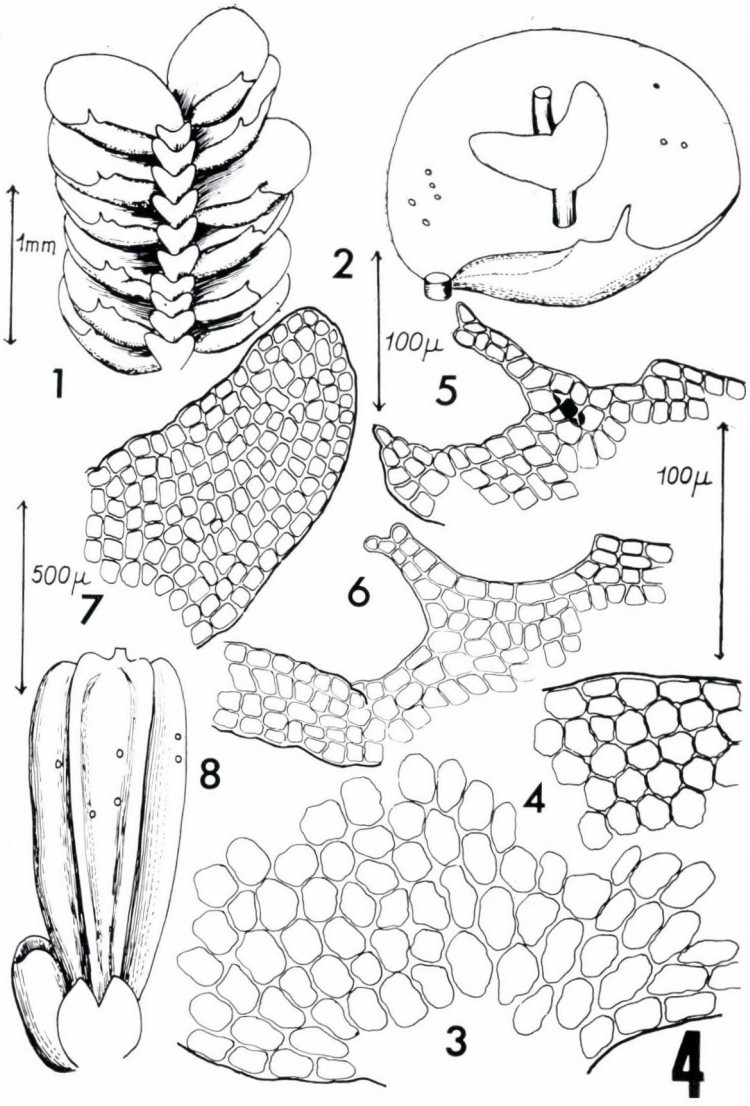


Fig. 4. — Diplasiolejeunea ensifera P. Tx. (holotype)
1: tige, 2: feuille, 3: bord du lobe, 4–7: lobule, 8: demi-amphigastre, 9: périanthe

très arquée, long de 1 mm, large de 0,9 mm. Lobule en sac, enflé, avec la marge supérieure récurvée, largement tronqué au sommet, long de 0,5 mm, large de 0,25 mm: dent apicale petite, dent médiane plus ou moins ciliée. Papille hyaline sur la face interne du lobule, longue de 50 μm. Amphigastres relativement petits avec des lobes courts et arrondis, hauts de 0,2 mm, larges de 0,3 mm. Plante dioïque. Inflorescence femelle à une innovation. Bractées périanthaires, à lobe et lobule égaux, longs de 0,5 mm, larges de 0,2 mm; bractéole bifide, haute de 0,2 mm. Périanthe cylindrique à 4 plis, à rostre marqué, haut de 1 mm, large de 0,5 mm.

Echantillons examinés: Tananarive, Andasibé, 1 400 m, sur branchettes en forêt de montagne, 10. 11. 1976, TIXIER 9626 (Holotype PC) — idem, Manjakandriana, Lac Mantasoa, villa Danièle, sur branchettes, 1 400 m, 1. 12. 1976, TIXIER 9989, 9991 — idem, Ankermakinda, 1 200 m, 10. 11. 1976, TIXIER 9042 — idem, La Mandraka, 1 200 m, 19. 6. 1977, TIXIER 10381 — idem, 29. 9. 1977, TIXIER 10936 — idem, Ambatoloana, 1 200 m, 4. 2. 1978, TIXIER 11148 — Tamatave, Antaniditra, 1 000 m, 19. 2. 1977, TIXIER 10333.

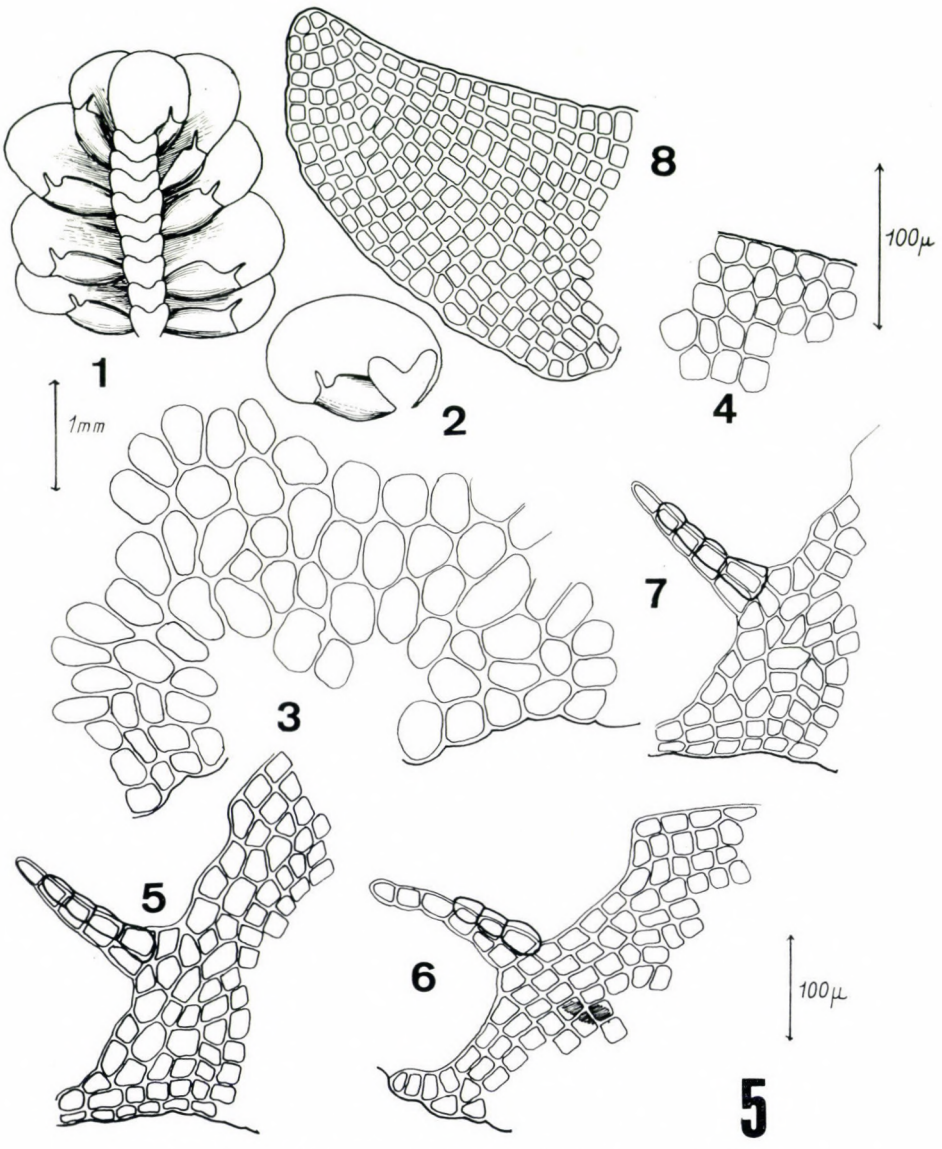


Fig. 5. — *Diplasiolejeunea phyllarthronii* P. Tx. (Route du Chrome)
1: tige, 2: feuille, 3: base du lobe, 4: apex du lobe, 5–7: apex du lobule, 8: demi-amphigastre

5. Diplasiolejeunea phyllarthronii P. Tx. sp. nov. (Fig. 5)

Planta corticola, magna, luteo-viridis, ad substratum appressa. Caules usque ad 1 cm longi, 120 μm crassi, cum foliis 2,5 mm lati. Folia interse 0,2 mm distantia, sub angulo 90° inserta. Cellulae foliorum, cuticula inermi, trigonis incrassionibusque intermediis visibilibus ad basin folii. Cellulae marginales, quadratae-rectangulares, 20×20 μm. Cellulae basales usque ad 40× 20 μm. Ocelli ad lobum plus aut minus multi (x = 18,5 ± 15). *Lobus elongatus, 1,6 mm longus, 1 mm latus, vix caulem tegens. Lobulus saccatus, carena elongata, inflata, 0,7 mm longus, 0,4 mm latus. Dens apicalis bene notata. Dens media, erecta, cum 3–4 ordinibus monocellularibus, pars duplex saepe brevior. Papilla hyalina, ovalis, 50 μm longa. Amphigastria, 0,5 mm lata, 0,5 mm alta, late bifida, lobis generaliter triangularibus. Folia propagulifera haud visa. Propaguli discoidei, rari, 120 μm in diametro, 40-cellulis. Cetera desunt.*

Echantillons examinés: Tananarive, Lac Mantasoa, 1400 m, corticole, 1, 12. 1976, Tixier 9516, 9812 (sur *Phyllarthron* sp.), 9991 — idem Andasibé, 1200 m, brousse secondaire en bordure de prairie marécageuse, 10. 11. 1976, Tixier 9162 — idem, La Mandraka, 1200 m, forêt de crête, 27. 9. 1972, Tixier 10953 — idem, Ambatoloana, 1200 m, forêt secondaire, 4. 2. 1978, Tixier 11140 — idem, Lac Mantasoa, 1400 m, 8. 6. 1978, Tixier 11856 — Tamatave, Manohitaly (Route du Chrome), 1 200 m, forêt basse de crête, 24. 3. 1978, Tixier 11632 (holotype, PC), 11763, 11792 — Fianarantsoa, Ambatofitorahana, 1 700 m, corticole en forêt, 29. 12. 1976, Tixier s. n. — idem, Vohiparara, 1 100 m, 24. 4. 1976, Tixier 12308.

Plante corticole, relativement grande, jaune-verdâtre, appliquée au support. Tige longue jusqu'à 1 cm, épaisse de 120 μm, large avec les feuilles de 2,5 mm. Feuilles distantes de 0,2 mm et insérées sous un angle de 90°. Cellules foliaires à cuticule lisse et à trigones et épaississements intermédiaires visibles vers la base de la feuille. Cellules de la marge, carrées-rectangulaires de 20×20 μm, cellules basales jusqu'à 40×20 μm. Ocelles sur le lobe généralement assez nombreux (x = 18,5 ± 15). Lobe allongé, oval, long de 1,6 mm, large de 1 mm, recouvrant à peine la tige. Lobule en sac, à carène allongée, plus ou moins gonflé, long de 0,7 mm, large de 0,4 mm. Dent apicale bien marquée (redan sur la marge supérieure du lobule). Dent médiane erectée, avec jusqu'à 4 étages de cellules monocellulaires, la partie double généralement plus courte, atteignant sur le type 4 cellules. Papille ovale, longue de 50 μm. Amphigastres, larges de 0,5 mm, hauts de 0,5 mm, largement bifides, à lobes généralement triangulaires, pas de feuilles propagulifères bien différenciées. Propagules discoïdes, rares, de 120 μm de diamètre et à 40 cellules. Fructification non observée.

6. Diplasiolejeunea palustrium P. Tx. sp. nov. (Fig. 6)

Planta corticola, luteo-viridis, ad substratum appressa. Caules usque ad 2 cm longi, 120 μm crassi, cum foliis 1,5 mm lati. Folia 0,2 mm interse distantia, sub angulo 90° inserta. Cellulae foliorum, cuticula inermi, trigonis incrassionibusque intermediis visibilibus ad basin folii. Cellulae marginales rectangulares, 20×15 μm, cellulae basales plus aut minus hexagonales usque ad 30×25 μm. Ocelli pauci aut multi. Lobus ovalis, elongatus, 0,9 mm longus, 0,6 mm latus, vix caulem tegens, sine sinu inter carenam marginemque posteriorem lobi. Lobulus saccatus, rotundatus, 0,5 mm longus, 0,2 mm latus. Dens apicalis haud visa. Dens media duplex brevior eadem D. phyllarthronii. Amphigastria 0,5 mm lata, 0,3 mm lata, lobis trapezoidibus. Propaguli haud visi. Flos masculus spicatus, lateralis, 1 mm altus cum bracteis 5-jugis monandris. Cetera desunt.

Echantillons examinés: Tananarive, Manjakandriana, Lac Mantasoa, 20. 10. 1976, Tixier 9275 — idem, Lac Tamatave, 4. 3. 1978, Tixier 11227 — Tamatave, Périnet, Antaniditra, 1 000 m bord de forêt marécageuse, 6. 7. 1977, Tixier 10636 (holotype *in coll. auct.*).

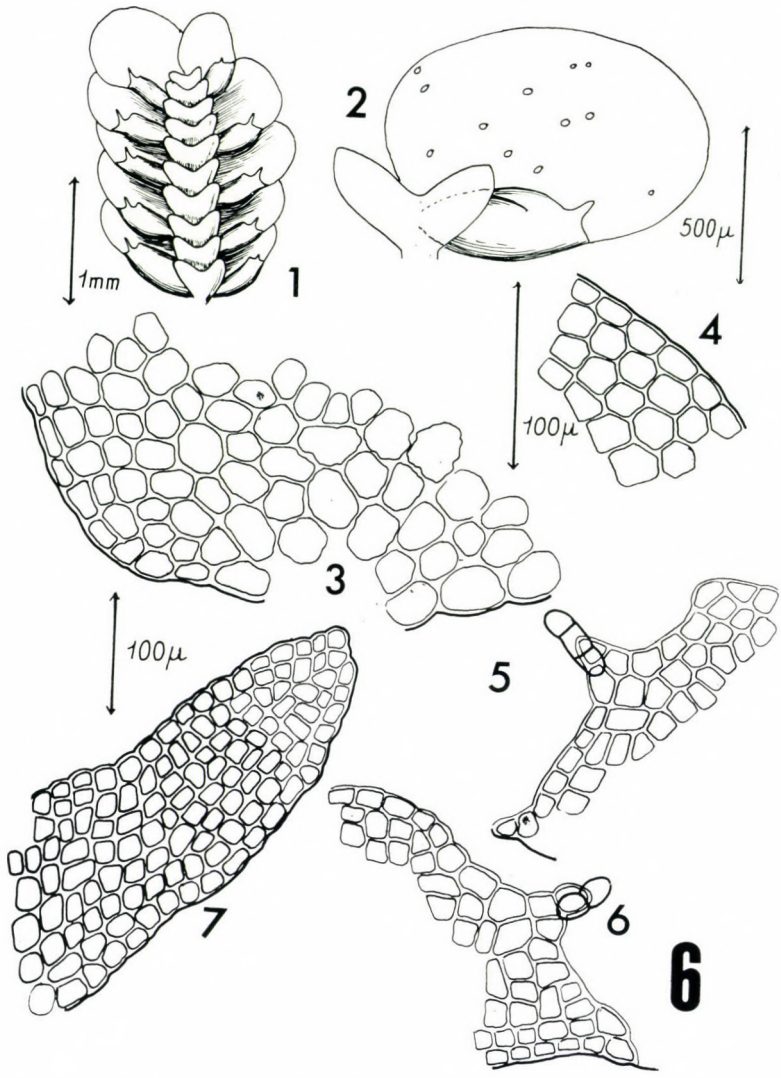


Fig. 6. — *Diplasiolejeunea palustrium* P. Tx. (Antaniditra)
1: tige, 2: feuille, 3: base du lobe, 4: apex du lobe, 5–6: apex du lobule, 7: demi-amphigastre

Plante corticole, vert-jaunâtre, plus ou moins appliquée au support. Tiges longues jusqu'à 2 cm, épaisses de 120 μm, larges avec les feuilles de 1,5 mm. Feuilles distantes entre elles de 0,2 mm, insérées sous un angle de 90°. Cellules foliaires, à cuticule lisse, trigones et épaississements intermédiaires visibles à la base de la feuille. Cellules de la marge du lobe, rectangulaires de 20×15 μm, cellules basales, plus ou moins hexagonales, jusqu'à 30×25 μm. Ocelles plus ou moins nombreux. Lobe oval-allongé, long de 0,9 mm, large de 0,6 mm, recouvrant à peine le lobe, sans sinus entre la marge inférieure de la feuille et de la carène. Lobule en sac plus ou moins arrondi, long de 0,5 mm, large de 0,2 mm. Dent apicale, nulle

ou peu marquée. Dent médiane double, plus courte que chez *D. phyllarthronii*. Amphigastres, larges de 0,5 mm, hauts de 0,3 mm, lobes plutôt trapézoïdaux. Propagules non observés. Epi mâle, latéral, haut de 1 mm et à 5 étages de bractées monandres. Le reste non observé.

Nous avons séparé, assez difficilement, cette espèce de *D. phyllarthronii* dans le but d'avoir un couple parallèle à celui *D. villaumei–D. jonesii*. L'agencement de la dent double demeure, malheureusement, assez variable (plus que chez *D. symoensii*). Rappelons que cette espèce se différencie de la précédente par le lobule oval à carène arrondie et à dent médiane courte.

7. **Diplasiolejeunea villaumei** Steph. (Fig. 7)

Spec. Hep. 5: 921, 1916.
SYNONYMES: *Diplasiolejeunea runssorensis* Steph. var. *australis* E. W. Jones, Trans. B.B.S. 7: 556, 1973.
ICONES: E. W. Jones, Trans. B.B.S. 7: 556, fig. 5, f–j, 1973.

Plante corticole, vert-jaunâtre, appliquée au support. Tiges longues jusqu'à 4 cm, épaisses de 120 μm, larges avec les feuilles de 2 mm. Feuilles distantes entre elles de 0,2 mm et insérées sous un angle de 90°. Cellules foliaires à cuticule lisse, trigones et épaississements intermédiaires visibles seulement à la base. Cellules marginales rectangulaires, 15–20 × 10 μm, cellules basales 60 × 40 μm. Lobule à carène allongée, long de 0,5 mm, large de 0,2 mm. Dent apicale marquée, dent médiane erectée ou arquée à 3–4 étages monocellulaires. Papille hyaline, ovale, de 40 μm en grand diamètre. Amphigastres larges de 0,5 mm, hauts de 0,3 mm, à lobes trapézoïdaux-triangulaires. Feuilles propagulifères sur un seul échantillon (11150). Propagules discoïdes de 90 μm de diamètre et à 40 cellules. Plante monoïque (fide Stephani). Inflorescence femelle à une innovation latérale, bractées périanthaires atteignant la moitié de la hauteur du périanthe à lobule un peu plus court, à apex arrondi, hautes de 0,5 mm, larges de 0,15 mm. Bractéole de la taille des bractées périanthaires, bifide au sommet. Périanthe à 5 plis, haut de 1,67 mm, large de 0,6 mm. Epis latéraux mâles à 7 étages de bractées diandres.

Echantillons examinés: Tananarive, Lac Mantasoa, 1 400 m, corticole, 1. 12. 1976, Tixier 9995 — idem, 29. 7. 1977, Tixier 10953 — idem, 11. 3. 1978, épiphylle, Tixier 11336, 11339, 11340, 11341, 11342, 11343, 11345 — idem, 6. 8. 1978, Tixier 11855 — idem, Ambatoloana, 4. 2. 1978, Tixier 11150a — idem, Anjozorobé, 1 000 m, corticole, 8. 12. 1976, Tixier 10024 — idem, Fehorana, 1 000 m, épiphylle, 2. 3. 1979, Tixier 12081 — idem, La Mandraka, 1 200 m, en forêt de crête, 13. 5. 1977, Tixier 10384 — idem, 22. 9. 1977, Tixier 10934 — idem, 22. 9. 1977, Tixier 11120, 11323 — idem, Ambatolampy, Manjakatompo, 1 700 m, 3. 11. 1976, Tixier s. n. — Tamatave, route de Lakato, 1 000 m, corticole, 2. 6. 1979, Tixier 12510, 12711 — idem, Analamazoatra, 1 000 m, Villaume s. n. (holotype, G).

8. **Diplasiolejeunea jonesii** P. Tx. sp. nov. (Fig. 8 & 9) Figs. 8—9.

Planta corticola, luteo-viridis, ad substratum appressa. Caules usque ad 1 cm longi, 120 μm crassi, cum foliis 2 mm lati. Folia interse 0,2 mm distantia, sub angulo 90° inserta. Cellulae foliorum, cuticula inermi, trigonis incrassionibusque intermediis visibilibus ad basin folii. Cellulae marginales plus aut minus isodiametricae, 20 × 20 μm metientes, cellulae basales, hexagonales, usque ad 30 × 20 μm. Lobus folii caulinaris, ovalis, rotundatus, vix caulem tegens, carena generaliter arcuata, lobus 1 mm longus, 0,8 mm latus. Lobus ovoideus, 0,5 mm longus, 0,15 mm latus. Dens apicalis haud visa, dens media brevis 1–3 ordinibus monocellularibus. Papilla hyalina, cum majore diametro 60 μm. Duo ordines foliorum propaguliferorum erectorum, propagulis ad apicem. Folia lobo majore quam eodem foliorum caulinarium, lobuboque longiore. Propaguli

ad marginem lobi usque ad 200 μm in diametro, 40 cellulis. Amphigastria bifida, 0,4 mm lata, 0,3 mm alta, lobis triangularibus. Planta dioica (specimenibus masculis vel femineis). Folia bractealia, apice rotundato, lobuloque breviore, 0,7 mm longa, 0,17 mm lata. Bracteola latebifida, 0,7 mm alta, 0,3 mm lata. Flos masculus spicatus cum bracteis 7 jugis, 0,5 mm latus.

Echantillons examinés: Tamatave, Antaniditra, 1 000 m, bordure de forêt marécageuse, 6. 7. 1977, TIXIER 10663 — Fianarantsoa, Manohaly, 1 200 m, 24. 3. 1978, TIXIER s. n. — idem, Vohiparara, 1 100 m, 30. 12. 1976, TIXIER 10157 (holotype, PC) — idem, TIXIER s. n.

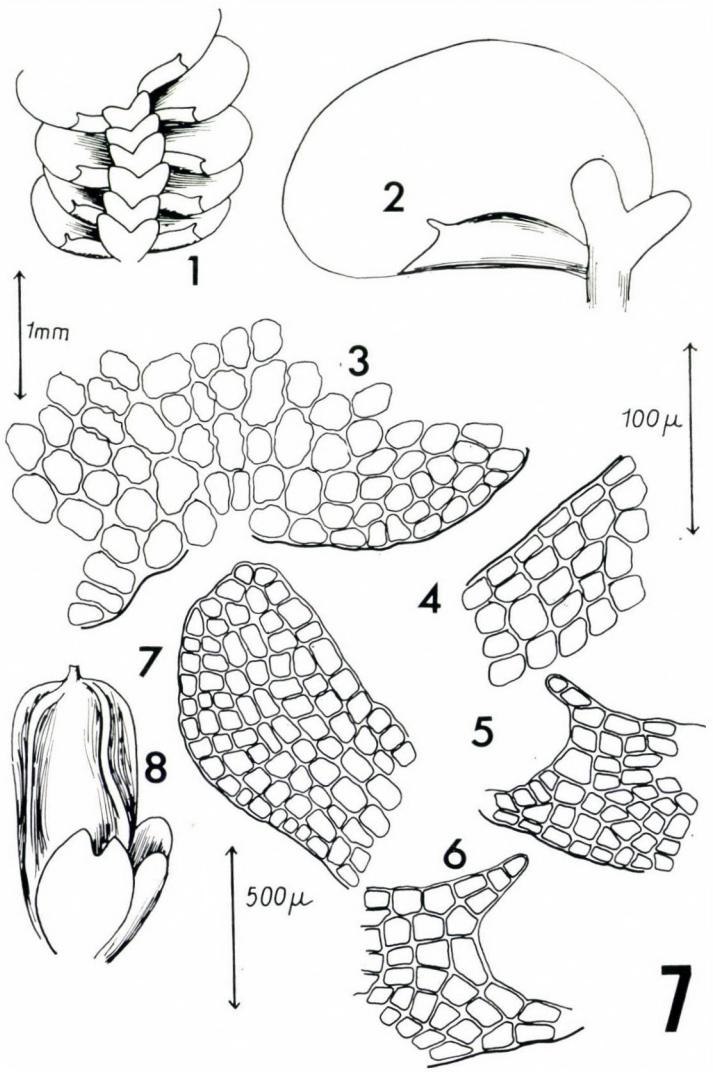


Fig. 7. — Diplasiolejeunea villaumei Steph. (holotype)
1: tige, 2: feuille, 3: base du lobe, 4: apex du lobe, 5–6: apex du lobule, 7: demi-amphigastre, 8: périanthe

Plante corticole, jaune verdâtre, appliquée au support. Tiges longues jusqu'à 2 cm, épaisses de 120 μm, larges avec les feuilles de 2 mm. Feuilles distantes entre elles de 0,2 mm et insérées sous un angle de 90°. Cellules foliaires à cuticule lisse, trigones et épaississements intermédiaires visibles à la base de la feuille. Cellules marginales, plus ou moins isodiamétriques de 20×20 μm, cellules de la base plutôt hexagonales et jusqu'à 30×20 μm. Lobe de la feuille arrondi, couvrant à peine la feuille, carène généralement courbe. Lobe long de 1,00 mm, large de 0,8 mm. Lobule généralement ovoïde, long de 0,5 mm, large de 0,15 mm, en sac. Dent apicale absente, le bord supérieur du lobe arrive par un arrondi à la dent médiane. Dent médiane courte, 1–3 étages monocellulaires, papille hyaline atteignant, dans son plus grand diamètre 60 μm. Il existe 1 à 2 étages de feuilles propagulifères, dressées perpendiculairement au support. Feuille propagulifère à lobe plus grand que sur les feuilles caulinaires et à lobule plus allongé. Propagules, situés à la périphérie de la feuille, atteignant jusqu'à 200 μm des diamètre et à une quarantaine de cellules. Espèce monoïque. Inflorescence femelle à une innovation latérale. Bractées périanthaires à lobe et lobule presque égaux et à apex arrondi (long de 0,7 mm, large de 0,17 mm). Bractéole bifide, haute de 0,7 mm, large de 0,3 mm. Epi mâle latéral.

Conclusions

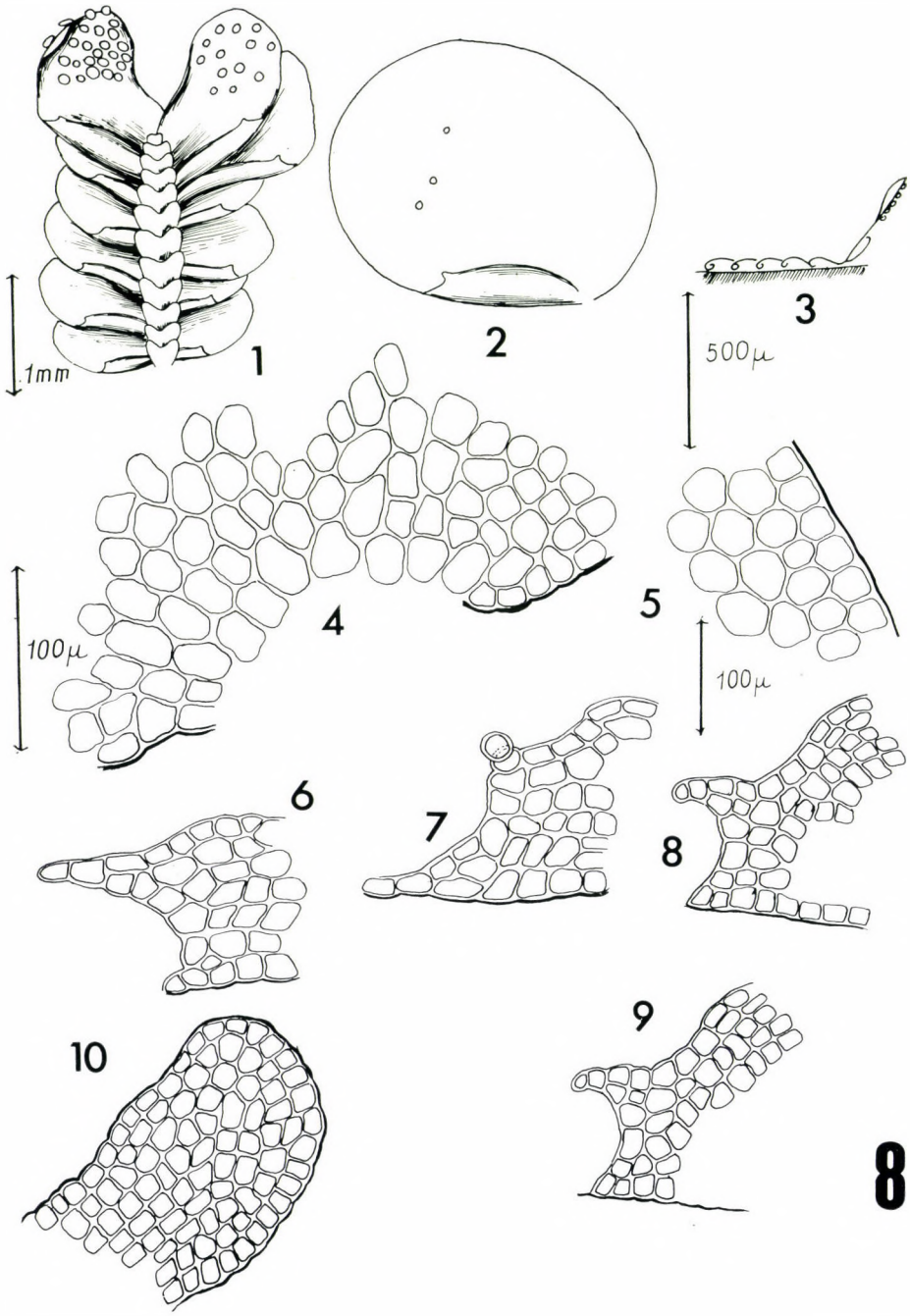
Cette section, sur le plan systématique, demeure avec la section *Cornutae*, celle dont l'analyse demeure la plus difficile. Bien que certaines espèces comme *D. symoensii* et *D. harpaphylla* demeurent des espèces stables dans toute leur aire de distribution et que d'autres comme *D. utriculata* et *D. kraussiana* différencient peu de taxons affins, la section *Villaumeae* pour Madagascar se résoud en huit espèces.

La variabilité de ces espèces demeure assez grande dans les limites envisagées, l'auteur restant prudent à la suite de son étude de *D. insignis* où les limites spacio-temporelles strictes ont mené à se limiter à une espèce unique.

Sur le plan biogéographique, la seule analyse qui semble valable revient à analyser l'étagement des espèces en altitude.

Au-dessus de 1 500 m	
Diplasiolejeunea insignis	1 650 m
Au-dessus de 1 200 m	
Diplasiolejeunea phyllarthronii	1 344,4 $\pm$ 157 m
Diplasiolejeunea palustrium	1 266,6 $\pm$ 188 m
Diplasiolejeunea jonesii	1 250 $\pm$ 166 m
Diplasiolejeunea ensifera	1 200 m
En dessous de 1 200 m	
Diplasiolejeunea villaumei	1 134,4 $\pm$ 418 m
Diplasiolejeunea lemuriana	1 125 $\pm$ 189 m

D. insignis se sépare du reste par son endémisme en altitude. *D. phyllarthronii* doit sa moyenne plus élevée par sa présence abondante vers 1 400 m au lac Mantasoa, les autres espèces restent dans la même gamme d'altitude avec la mention que *D. lemuriana* est l'espèce récoltée le plus bas.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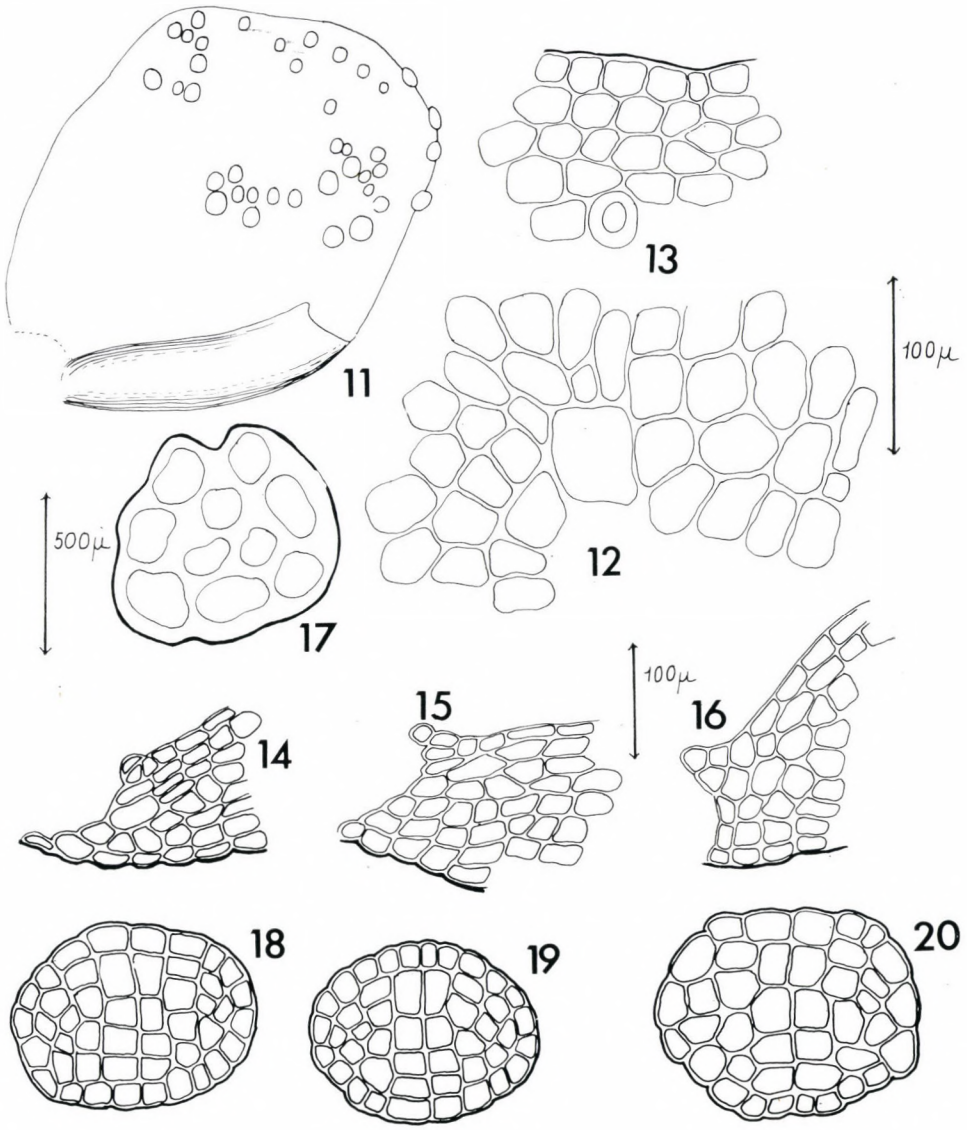

Figs 8–9. — *Diplasiolejeunea jonesii* P. Tx. (Vohiparara)
1: tige, 2: feuille, 3: port de la tige, 4: base du lobe, 5: apex du lobe, 6–9: apex du lobule, 10: demi-amphigastre, 11: feuilles propagulifères, 12: base du lobe, 13: apex du lobe, 14–16: apex du lobule, 17: coupe de la tige, 18–20: propagules

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REVISIÓN DEL GÉNERO *MACHAONIA* H. ET B. (RUBIACEAE) EN CUBA*

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(Llegado: 15. Septiembre, 1981)

A critical re-examination of the taxa of the genus *Machaonia* existing in Cuba contains detailed descriptions of 13 species, 9 subspecies and 2 forms and an analytic key for their determination. Among them some are new to the science: *Machaonia Acunae*, *M. dumosa*, *M. micrantha*, *M. nipensis*, *M. pubescens*, *M. havanensis* ssp. *orientalis*, *M. nipensis* ssp. *moaensis*, *M. pauciflora* ssp. *glabrata*, *M. subinermis* ssp. *armata*, *M. dumosa* f. *pilosa*. *M. variifolia* proved to be a synonym of *M. microphylla* Griseb. and *M. trifurcata* Urb. has been transferred to *M. pauciflora* as its subspecies. The authors found 4 vicariant species of wider distribution: *M. havanensis*, *M. pauciflora*, *M. subinermis* and *M. microphylla*. The other 9 species are also vicariant but with more reduced areas, some of them (*M. Acunae*, *M. dumosa*, *M. pubescens*, *M. urbinoi*) seem to be local endemics. All the species investigated are endemics to the flora of Cuba.

Introduccion

El género *Machaonia* H. et B. siempre se condideró, como uno de los mas difíciles, en cuanto a la clasificación de sus espécies y la caracterización morfológica correcta de ellas. Sobre todo las espécies espinosas y de hojas pequeñas, de las Antillas presentaron muchas dificultades a los taxónomos por la gran variabilidad en sus portes, espinosidad, forma y tamaño de las hojas, forma, tamaño y pelosidad de los frutos.

La primera espécie cubana de este género fue descrita por GRISEBACH en 1862 (*M. microphylla*) y en el Catálogo (1866) listaba otra bajo el nombre: *M. cymosa* URBAN (1908) revisando los materiales colectados en las Antillas, encontró, que *Machaonia cymosa* Griseb. es una planta endémica de Jamaica, y la espécie cubana la describió como nueva, bajo el nombre de *M. trifurcata* Urb. El mismo autor encontró en las colectas Wrightianas otro taxon que describió con antelación, como *M. pauciflora*. BRITTON (1916) añadió la descripción de otras dos espécies bajo los nombres: *M. calcicola* y *M. littoralis* y confeccionó la primera clave analítica para las espécies cubanas. En el transcurso de los años 1920–1934 se publicaron otras 4 espécies: *M. minutifolia* Britt. et Wils, *M. variifolia* Urb., *M. subinermis* Urb., *M. tiffina* Ekm. et Urb. STANDLEY (1934) en North American Flora realizó la primera síntesis del género del territorio correspondiente, elaborando una clave basada mayormente en los caracteres del tamaño de la corola y fruto. En el mismo trabajo publicó otra espécie cubana: *M. urbaniana*. ALAIN (1964) confeccionó una clave basada principalmente en tamaño y pelosidad del fruto, y redujo en la sinonimía dos espécies descritas por BRITTON.

En este trabajo todos los taxa tienen la revisión y caracterización en base a la investigación del holotipo de cada uno. Los autores pretendieron incluir rasgos vegetativos importantes en la clave y caracterización, y dieron importancia a los rasgos morfológicos de la corola. Añadieron la descripción de 5 espécies y 4 subespécies nuevas y redujeron 2 espécies

* Rubiáceas Cubanas IV.

en la sinonimía. Encontraron, que en Cuba hay 4 espécies vicariantes de mayor distribución, *M. havanensis*, *M. pauciflora*, *M. subinermis* y *M. microphylla*. Las demás 9 espécies, también vicariantes tienen distribución mas reducida, algunas de ellas areas puntiformes.

Clave para las especies cubanas:

1 a Hojas de 2–7 mm de largo, sin nervios laterales conspicuos en las ramas leñosas (en las ramas juveniles con hojas más grandes, rómbeas, con un par de nervios laterales) 10
b Hojas mayores (pequeñas en *M. tiffina* y *M. Acunae*) con nervios laterales conspicuos, mayormente promínulos 2
2 a Hojas pubescentes o hirsutas en ambas caras 3
b Hojas lampiñas, a veces domaciadas en el ángulo de los nervios laterales 5
3 a Hojas elípticas a suborbiculares de 3–6 mm de largo, hirsutas con pelos rígidos de base engrosada, nervios laterales prominentes y reticulados en el haz ..... **7. M. Acunae**
b Hojas aovadas a oblongo-elípticas de hasta 15 mm de largo, pubérulas a pubescentes con pelos suaves 4
4 a Lóbulos del cáliz suborbiculares, fruto obovado con base redondeada; las ojas densamente pubescentes ..... **1. M. pubescens**
b Lóbulos del cáliz triangulares, fruto obtriangular con base aguda o retusa; hojas domaciadas, pubérulas mayormente en los nervios .... **2a. M. havanensis ssp. havanensis**
5 a Hojas pequeñas, obovadas de 3–6 mm de largo, cáliz y fruto lampiños ..... **9. M. tiffina**
b Hojas mas grandes 6
6 a Hojas con domacias pubescentes en los ángulos de los nervios laterales del envés 7
b Hojas sin domacias 8
7 a Flores blancas, cáliz y hipantio muy hirsutos, lóbulos mas cortos que el hipantio; corola pubescente por fuera ..... **3. M. microphylla**
b Flores rosadas, muy pequeñas; lóbulos del cáliz glabrescentes a glabros, mas largos que el hipantio, corola lampiña ..... **4. M. micrantha**
8 a Lóbulos del cáliz redondeados, fruto siempre peloso a hirsuto, obovado redondeado en la base ..... **5. M. subinermis**
aa Hojas lineal-obovadas, ramitas ± inermes ... **5a. ssp. subinermis**
bb Hojas elípticas a rómbeas; ramitas con espinas mayormente ramificadas ..... **5b. ssp. armata**
b Lóbulos del cáliz triangulares, agudos a obtusos fruto agudo a retuso en la base, lampiño cuando redondeado 9
9 a Tubo y lóbulos del cáliz hirsutos, fruto agudo en la base .... **2b. M. havanensis ssp. orientalis**

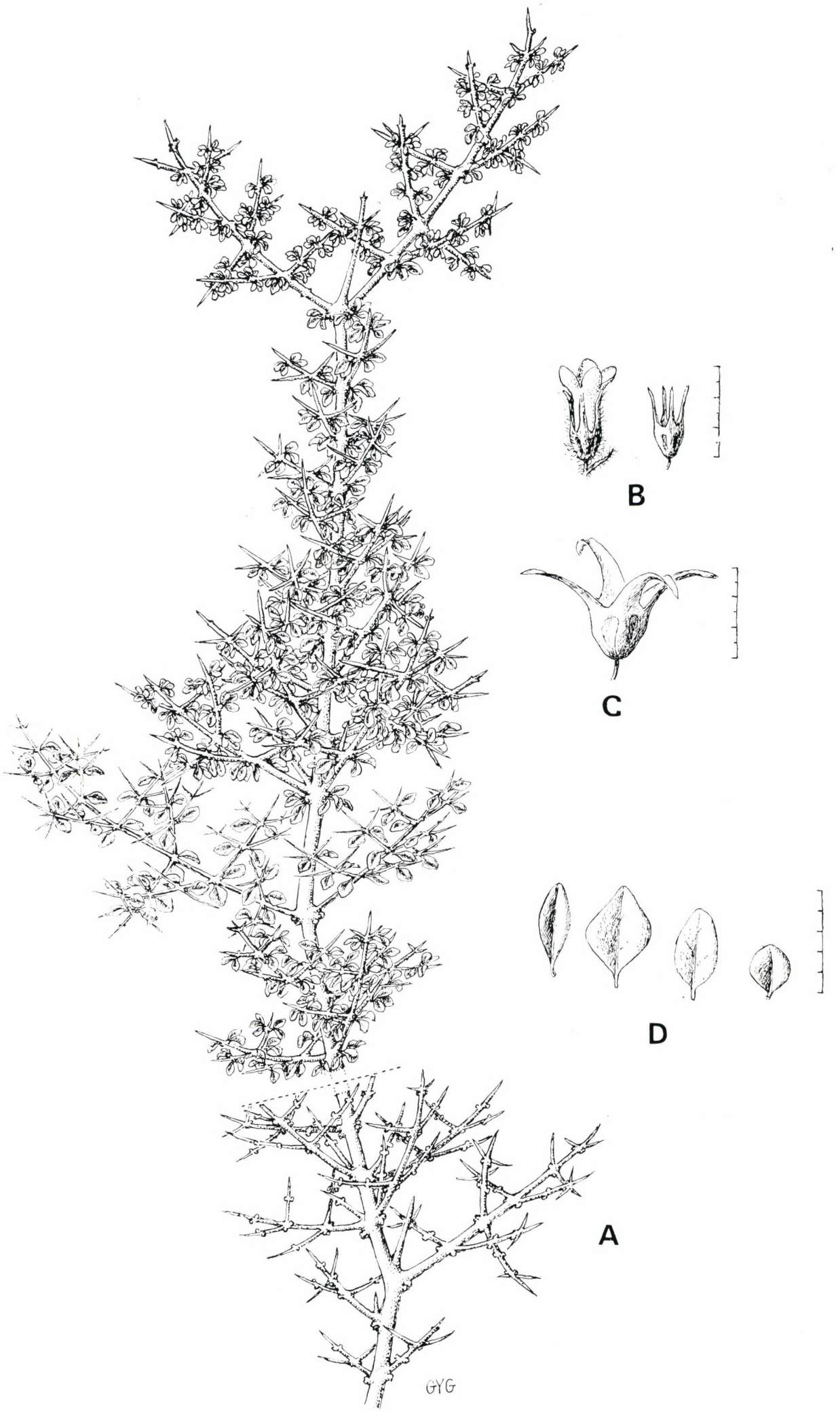

Fig. 1. Machaonia dumosa Borhidi et Fernandez; A: Aspecto general; B: flor; C: fruto; D: Hojas. Escalas 3 y 5 mm. (Dibujo de Gisela GYURKÓ)

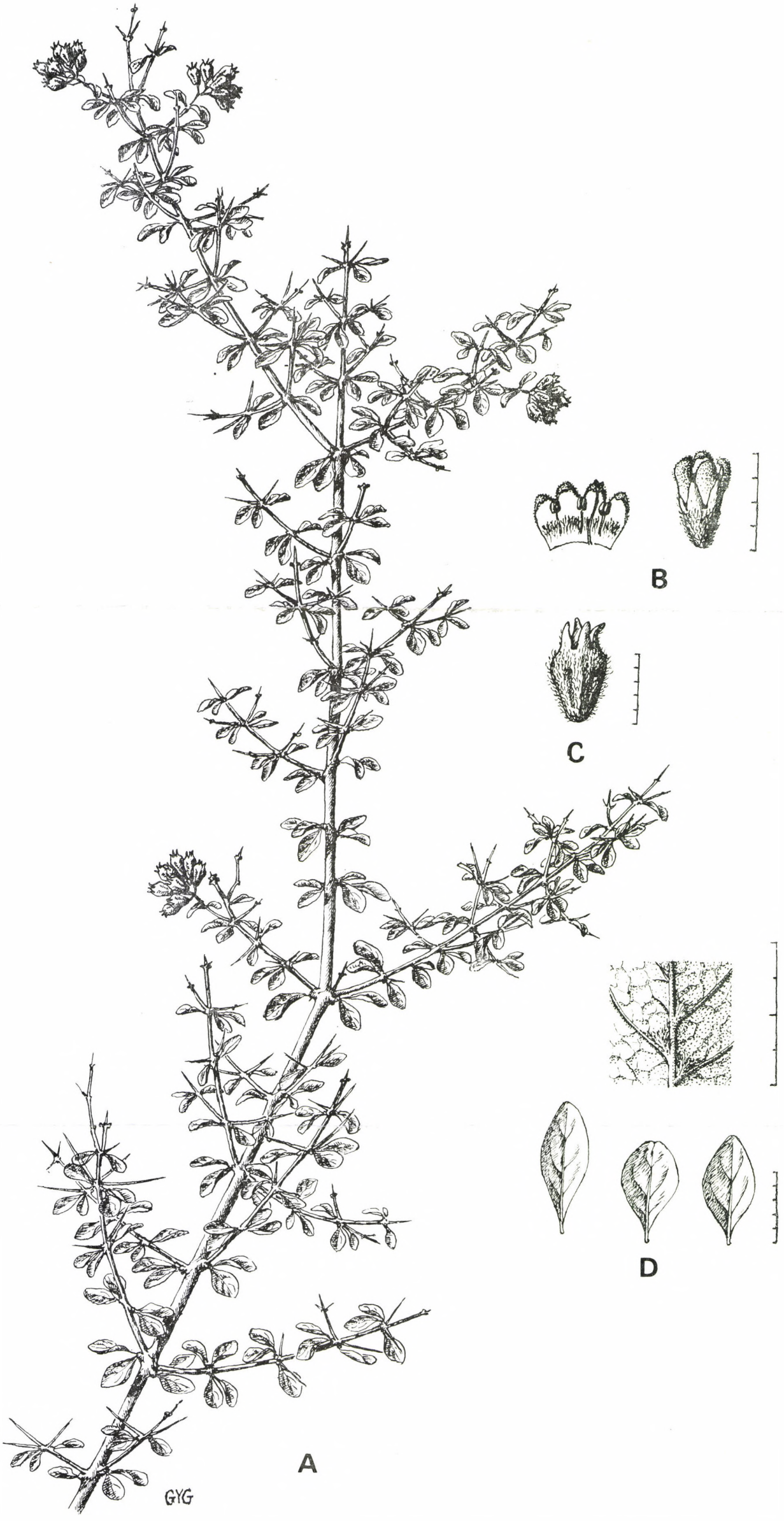

Fig. 2. Machaonia micrantha Borhidi et Fernandez; A: Aspecto general; B: Flor y sección de la corola; C: Fruto; D: Hojas. Escalas: 5 y 3 mm. (Dibujo de Gisela GYURKÓ)

b Tubo del cáliz lampiño a deprimido-peloso, lóbulos lampiños a ciliados en el margen ..... **6. M. pauciflora**

aa Hojas brillantes en el haz, nervios promínulos cc
bb Hojas mates en el haz nervios no promínulos, cáliz y hipantio glabros ..... **6b. ssp. glabrata**
cc Cáliz y hipantio glabros, ramitas mayormente inermes .... **6a. ssp. pauciflora**
dd Hipantio deprimido-peloso, lóbulos del cáliz ciliados; ramas mayormente espinosas ..... **6c. ssp. trifurcata**

10 a Hojas 4–7 mm de largo, oblongo-obovadas, densamente pubescentes en ambas caras con pelos cortos suaves ..... **8. M. urbaniana**
b Hojas glabras o esparcidamente estrigiloso-pelosas en el haz 11

11 a Hojas orbiculares a suborbiculares, carnoso-coriáceas, mates y rugulosas cuando secas, hipantio y fruto deprimido-pelosos ..... **10. M. nipensis**
aa Corola blanca, 3–4 mm de largo ..... **10a. ssp. nipensis**
bb Corola rosada, 1.5–2.5 mm de largo ..... **10b. ssp. moaensis**
b Hojas obovadas, coriáceas y brillantes en el haz o cartáceas mates y conduplicadas; hipantio y fruto glabros 12

12 a Plantas mayormente inermes, con ramitas delgadas, flexuosas; hojas conduplicadas y mates en el haz, pequeñas; rómbeas y planas en las ramas juveniles ..... **11. M. minutifolia**
b Plantas muy espinosas con espinas gruesas y ramificadas; hojas coriáceas y brillantes en el haz 13

13 a Lóbulos del cáliz 5, mas cortos que el hipantio oblongo-obovado de 5–6 mm de largo, agudo en la base ..... **12. M. urbinoi**
b Lóbulos del cáliz 4, lineales o lineal-lanceolados mas largos que el hipantio semiorbicular de 1.5–2 mm de largo, redondeado en la base ..... **13. M. dumosa**
aa Hojas lampiñas ..... **13a. f. dumosa**
bb Hojas estrigilosas en el haz ..... **13b. f. pilosa**

Machaonia Acunae Borhidi et Fernandez sp. n.

Frutex spinosus, dense ramificatus. Rami hornotini 4-anguli, circumcirca breviter strigilloso-hirsuti, veteriores teretes, glabri, internodiis 1–1,5 cm longis suffulti, laterales in spinas simplices vel breviter trifurcatas, 0,5–1 cm longas excurrentes. Folia in nodis fasciculata, elliptica vel obovata, rariter suborbiculata, antice rotundata, basi angustata et in petiolum 0,2–0,5 mm longum protracta, 3–7 mm longa et 2–5 mm lata, nervo medio supra prominulo, subtus leviter impresso, lateralibus, utroque latere 2–3, supra prominulis et dense reticulatis, subtus impressis et ante marginem conjunctis, non reticulatis; lamina pilis rigidis, basi incrassatis scaberulo-hirsuta, supra nitida, subtus opaca, chartacea vel subcoriacea.

Inflorescentiae terminales corymbosae 5–15-florae dense hirsutae. Calyx 2 mm longus, tubus obovatus 1 mm longus, lobi 1 mm longi, ovato-lanceolati, acuti vel obtusi cum

tubo patenter hirsuti. Corolla 2 mm longa, extus hirsuta, tubus 1,5 mm longus, lobi 4, triangular-ovati, 0,5 mm longi, extus hirsuti; faux corollae cum parte superiori tubi corollini intus villosa, basi glabra; stamina 4 in sinubus tubi corollini sessiles, antherae suborbiculares. Stylus 2 mm longus, pilosus, stigma breviter bilobatum. Fructus in sicco rubellus, obpyramidalis, 2,5–3 mm longus, hirsutus, basi obtusus vel breviter rotundatus, lobi calycini 1–1,2 mm longi triangulares vel ovati, obtusi, margine strigillosi.

Holotypus: Roig 12891 HAC; Isla de la Juventud; Sabana Presidio Modelo al E. de Nueva Gerona. Leg.: J. T. Roig 25. 8. 1945.

Arbusto espinoso, densamente ramificado. Ramitas 4-angulosas, brevemente estrigiloso-hirsutas, adultas cilindricas, glabras, entrenudos de 1–1.5 cm de largo, ramas laterales a menudo terminantes en espinas sencillas o brevemente trifurcadas, de 0.5–1 cm de largo. Hojas fasciculadas en los nódulos, elípticas u obovadas, raramente suborbiculares, redondeadas en el ápice, atenuadas en la base hacia el pecíolo de 0.2–0.5 mm de largo, limbo de la hoja de 3–7 mm de largo y 2–5 mm de ancho, nervio medio promínulo en el haz, ligeramente hundido en el envés, los laterales 2–3 pares promínulos y densamente reticulados en el haz hundidos y anastomosados al margen, pero no reticulados en el envés; el limbo escabroso-hirsuto en ambas caras con pelos rígidos, engrosados en la base, brillante en el haz, mate en el envés, cartáceo o subcoriáceo.

Inflorescencias terminales, corimbosas, 5–15-floras, densamente hirsutas. Cáliz de 2 mm de largo, obovado, el tubo de 1 mm, los lóbulos también de 1 mm de largo, aovado-lanceolados agudos u obtusos junto con el tubo hirsutos. Corola de 2 mm de largo, hirsuta por fuera, el tubo de 1.5 mm, los lóbulos de 0.5 mm de largo, peloso por fuera; garganta y la parte superior del tubo de la corola vellosa por dentro, la base glabra. Estambres 4, anteras en los senos de la corola sésiles, suborbiculares. Estilo de 2 mm de largo, peloso, el estigma brevemente bilobulado. Fruto rojizo cuando seco, obpiramidal, de 2.5–3 mm de largo, hirsuto, obtuso o brevemente redondeado en la base, lóbulos del cáliz de 1–1.2 mm de largo, triangulares o aovados, obtusos, ciliados en el margen.

Holotipo: Roig 12891 HAC; Isla de la Juventud; Sabanas Presidio Modelo, al E. de Nueva Gerona. Col.: J. T. Roig, 25. 8. 1945.

Esta espécie fue clasificada como *M. trifurcata* Urb. de la cual se distingue claramente en tener ramitas, hojas e inflorescencias hirsutas, corola y fruto hirsutos; conocida sólo de la colecta tipica.

Machaonia dumosa Borhidi et Fernandez sp. n. (Fig. 1)

Frutex usque ad 2 m altus, valde ramosus, rami spinosi, spinas bi- vel trifurcatis, juvenilibus ferrugineo-pilosis suffulti, ramuli scabrosi et breviter ferrugineo-pilosi, demum glabri. Stipulae 0,5–0,8 mm longae, late ellipticae, abrupte apiculatae, pilosulae. Folia opposita vel verticillata ± 1 mm longe petiolata, petiolis breviter pilosis suffulta, obovata vel obovato-elliptica vel ovata, 2,5–7 mm longa et 2–4 mm lata, apice rotundata vel obtusa, rariter apiculata, basi attenuata et cuneata, subcoriacea; supra nitida glabra, rariter pilosa, nervo medio subtus prominente, apicem versus attenuato et impresso demum evanescente, laterales utrinque nulli. Inflorescentiae axillares, cymosae 1–3-florae, subsessiles. Tubus calycis cca. 1 mm longus semiorbicularis, basi rotundatus, breviter pilosus; lobi 4, lineari-lanceolati, acuti vel obtusiusculi, 2–3 mm longi, margine plerumque longe ciliati. Corolla non visa. Fructus 1,5–2 mm longus, et 2 mm latus, late obovatus, glabrescens vel glaber; lobi calycis persistentes, plerumque reflexi, 2–3 mm longi, tubum superantes.

Holotypus: 28049 HAC; Cuba; Prov. Pinar del Rio. In fruticetis serpentinosis aridis montis Loma Preluda de Cajalbana. La Palma. Leg.: A. Borhidi et R. Capote 28. 1. 1976. Isotypus: BP.

f. dumosa: foliis supra glabris

f. pilosa Borhidi et Fernandez f. n.

foliis supra pilis rigidis suffultis.

Holotypus: 28050 HAC; Cuba; Prov. Pinar del Rio. In fruticetis serpentinosis cacuminis montis La Cajalbana, alt. approx. 470 m.s.m. La Mulata; Leg.: A. Borhidi, 20. 12. 1975. Isotypus: BP.

Arbusto de hasta 2 m de altura, de ramas muy espinosas; espinas rectas, bi- o trifurcadas, ramitas escabrositas y corto pelosas con pelos diminutos ferrugineos, luego glabras. Estípulas anchamente elípticas, abruptamente apiculadas de 0.5–0.8 mm de largo, pelositas; hojas opuestas a verticiladas con pecíolo de ± 1 mm de largo, brevemente peloso, obovadas a obovado-elípticas u ovadas de 2.5–7 mm por 2–4 mm, redondeadas a obtusas, a veces apiculadas en el ápice, estrechadas a cuneadas en la base, el haz brillante y glabro — a veces peloso, el envés glabro; nervio medio prominente en el envés estrechando y hundiendose hacia el ápice, nervios laterales nulos en ambas caras, el limbo subcoriáceo. Inflorescencia cimosa, 1–3-flora, subsésil en las axilas. Tubo del cáliz de 1 mm, semiorbicular, redondeado en la base, corto peloso; lóbulos 4, lineal-lanceolados, aguditos a obtusos de 2 mm de largo, por lo comun largamente ciliados en el margen debajo de la mitad. Fruto anchamente obovado de 1.5–2 mm de largo, glabrescente a glabro, lóbulos del cáliz persistentes, de 2–3 mm de largo, mayormente reflejos. Semillas 2, anchamente elipticas de 1–1.3 mm de largo, comprimidas ventralmente, pardo-rojizas. Corola no vista.

Holotipo: 28049 HAC; Cuba; Prov. Pinar del Rio. En cuabales de la Loma Preluda de Cajálbana, La Palma. Col.: A. Borhidi y R. Capote, 28. 1. 1976. Isotipo: BP.

forma **dumosa:**

hojas glabras en el haz

forma **pilosa** Borhidi y Fernandez f. n.

hojas con pelos rigidos en el haz.

Holotipo: 28050 HAC; Cuba; Prov. Pinar del Rio. En los cuabales de la cumbre de la Loma de Cajálbana, en aprox. 470 m. de altura, La Mulata. Col.: A. Borhidi, 20. 12. 1975. Isotipo: BP.

Ejemplares examinados: Prov. Pinar del Rio: Loma Preluda de Cajálbana, suelo serpentinoso, Borhidi et Capote 14002; HAC; BP; — Idem: 4570 HAJB, leg.: Bisse et Rojas; — Idem: 18302 HAJB, leg.: Bisse et Lippold. — Cumbre rocosa de la Loma Cajálbana, 470 m s. n. m. leg.: Borhidi, Capote et Del-Risco 28301 HAC, BP. (7998). — In pinetis lateriticis cymo montis Cajálbana supra La Mulata 470 m s. n. m. leg.: Borhidi 5. 7. 1970, BP.

Esta espécie es afin a *Machaonia nipensis* Borhidi y Fernandez, de la cual se distingue en tener hojas coriáceas brillantes y a veces venosas en el haz, lóbulos del cáliz lineal lanceolados, más largos que el tubo; y hipantio glabro. Es una espécie endémica de los matorrales serpentinosos de la Sierra de Cajálbana.

Machaonia havanensis (Jacq.) Alain

(Basionymon: *Spermacoce havanensis* Jacq.; J. F. Gmelin Syst. Nat. 234. — Syn.: *Spermacoce spinosa* Jacq. Sel. Stirp. Amer. **21:** 7, 1763, non *Spermacoce spinosa* L.; — *Machaonia calcicola* Britt. Bull. Torr. Bot. Club **43:** 453, 1916)

Arbusto o arbolito de hasta 3–4 m de alto. Ramitas espinosas y brevemente hírtulas. Estípulas diminutas, triangulares, pubérulas, obtusas; hojas aovadas, rómbico-aovadas a elíptico-oblongas, a veces oblanceoladas u obovadas, de 6–15 mm de largo por 3–10 mm de ancho, acuminadas y obtusas en la base, obtusas a aguditas en el ápice, a veces redondeadas; glabras o mayormente pelosas en los nervios en ambas caras, membranáceas a cartáceas. Nervios laterales 2–3 pares en ambas caras, visibles, con domacias pubérulas en los ángulos, a veces ausentes.

Inflorescencia en cimas terminales paucífloras. Cáliz densamente pelósito, el tubo de 1 mm de largo, lóbulos 4, de 0.7–1 mm de largo, triangulares o aovados, obtusos a aguditos en el ápice. Corola blanca o amarillenta, pulverulenta a glabra por fuera, lóbulos 4, redondeado-aovados. Fruto obpiramidal, hirsuto, de 3–4 mm de largo, atenuado en la base agudo u obtuso.

ssp. **havanensis**

Con hojas membranáceas a subcartáceas, mates en el haz, pubérulas en los nervios, domaciadas en el envés.

Vive en los mogotes calizos y en los matorrales litorales de las calizas costeras, en Pinar del Rio, Habana y Matanzas.

Ejemplares examinados: Cuba; Ramón de la Sagra 229. ex Herb. Mus. Paris. Field Mus. 654015. — PINAR DEL RIO; Bahia de Corrientes leg.: Britton y Cowell 9894, 10–12. 3. 1911 NY; — Pinar del Rio: Loma de la Finca El Mameyal. Leg. Acuña 24657 HAC; 1936. — Pinar del Rio: Pan de Guajaibón, HAJB 32573, Bisse y otros; Idem: Borhidi y Capote 8. 1. 1976, HAC; — PROV. HABANA: Sierra de Anafe Ekman 16910 S, — Idem: León 11618 NY, HAC; — Idem: Alain 5319 NY, HAC; — Idem: León et Roca 8821 HAC; — Idem: Alain 6016 HAC; — Idem: Acuña et Roig 21672 HAC; — Idem: León 2830 HAC; — Idem: Wilson 11341 US, NY; — Idem: P. Wilson et León 11462 F, NY; — Habana, El Morro al Este, Cueva de los Camarones, León 7592 US, HAC; — Prov. Habana: Loma del Pache, Tapaste; León 7331 GH, NY, HAC; — PROV. MATANZAS: Pan de Matanzas cca 400 m s. n. m. Ekman 16456 S, GH, NY.

ssp. **orientalis** Borhidi et Fernandez ssp. n.

A typo differt: foliis chartaceis, supra nitidis, utrinque glabris, subtus sine domatiis.

Holotypus: Acuña 17148 HAC; Prov. Tunas (Oriente); Sabanas del Central Manati. Leg.: Acuña 24. 11. 1951. Isotypus: NY.

Difiere del tipo en tener hojas cartáceas, brillantes en el haz, glabras en ambas caras, sin domácias en el envés.

Holotipo: Acuña 17148 HAC; Prov. Tunas; Sabanas del Central Manati. Col.: Acuña 24. 11. 1951. Isotipo: NY.

Ejemplares examinadas: PROV. TUNAS (Oriente); Manigua costera cerca del Faro, Bahia de Manati, León 16686 HAC; — Prov. Tunas: Puerto Padre; manigua de terrenos malos, El Cupey, La Yaya; Roig 5078, 5079 (Curbelo 514) HAC.

Discusión: Esta espécie se segrega en dos subespécies bien distinguida morfológica mente, con areas claramente separadas. Sus poblaciones se encuentran mayormente en la costas rocosas de caliza y en los mogotes cercanos al mar, a lo largo de las costas del Norte de Cuba, en las provincias de Pinar del Rio, Habana, Matanzas y Tunas.

Machaonia micrantha Borhidi et Fernandez sp. n. (Fig. 2)

(Syn.: *Machaonia microphylla* Griseb. sensu Alain p.p.)

Frutex usque ad 1,5 m altus, breviter ramosus; rami laterales plerumque subinermes vel in inflorescentias vel in spinas simplices, rariter trifurcatas, 0,5–1,5 cm longas excurrentes, hornotini 4-angulares, dense breviterque strigilloso-puberuli, veteriores teretes, postremo glabri. Stipulae triangulares, 0.5 mm longae, mucronato-acutae, dorso puberulae, apice ipso glabro. Folia sessilia vel subsessilia, suborbicularia, obovata vel late rhombea, antice rotundata, basi longe vel breviter angustata, 4–14 mm longa et 3–10 mm lata, nervo medio supra plano vel leviter impresso, subtus prominente, lateralibus utroque latere 1–2, arcuatis, supra leviter prominulis, subconspicuis, subtus impressis; lamina supra nitida, glabra, subtus pallidior, nitidula, in angulis venarum lateralium pubescenter domatiata, chartacea.

Inflorescentiae terminales, breviter et dense racemosae, multiflorae. Calyx oblongo-obovatus, 2–2,2 mm longus, basi rotundatus, tubus calycis semiorbicularis, usque ad 1 mm longus, dense hirsutus, lobi calycis 4, oblongo-ovati vel lineari-ovati, apice rotundati, tubo calycino paullo longiores, 1–1,3 mm longi, sparse hirsuti. Corolla 1,5–2 mm longa, tubus corollae 0,7–1 mm longus e lobis calycinis non exsertus, extus glaber, intus villosus, faux ipsa glabra, lobi corollae tubo aequilongi vel longiores, utrinque glabri. Stamina 4, filamenta in tercio inferiore tubi corollini affixa, 0,4–0,7 mm longa, antherae subglobosae, in sinubus loborum corollae insertae. Stylus 2 mm longus, glaber, apice capitatus. Fructus 5–6 mm longus et 3–3,5 mm latus, basi obtusus vel rotundatus, levissime sulcatus, puberulus, lobi calycini persistentes 1–2 mm longi, apice rotundati.

Holotypus: CLEMENTE 6908 HAC; Cerro de Cananova, Moa. Leg.: CLEMENTE, ALAIN et CRYSÓGONE, jul. 1949. Isotypus: ALAIN 1010 US, NY.

Arbusto de hasta 1.5 m de alto. Ramitas laterales subinermes o terminadas en inflorescencias o en espinas sencillas o raramente trifurcadas de 0.5–1.5 cm de largo. Ramas adultas cilindricas, glabras, las jóvenes 4-angulosas, densamente estrigiloso-pubérulas. Estípulas triangulares de 0.5 mm de largo, mucronadas en el ápice, pubérulas, el mucrón glabro. Hojas sésiles o subsésiles, suborbiculares, obovadas o anchamente rómbeas, redondeadas en el ápice, brevemente atenuadas en la base, de 4–14 mm de largo y 3–10 mm de ancho; nervio medio aplanado o poco hundido en el haz, prominente en el envés, los laterales 1–2 pares encorvados hacia el ápice, ligeramente promínulos en el haz, hundidos en el envés. El limbo brillante y glabro en el haz, pálido y mas mate en el envés, con domácias pubescentes en los ángulos de los nervios laterales, cartáceo.

Inflorescencias terminales, corto y densamente racemosas, multífloras. El cáliz oblongo-obovado, de 2–2.2 mm de largo, redondeado en la base, el tubo semiorbicular de hasta 1 mm de largo, densamente hirsuto; lóbulos del cáliz 4, oblongo-aovados lineal-aovados, redondeados en el ápice, poco más largos que el hipantio, esparcidamente hirsutos. Corola de 1.5–2 mm de largo, el tubo de 0.7–1 mm de largo, no saliendo de los lóbulos del cáliz, glabro por fuera, velloso por dentro, la garganta glabra; los lóbulos de igual largo o mas que el tubo, glabros en ambas caras. Estambres 4, filamentos adnatos en el tercio inferior del tubo, de 0.4–0.7 mm de largo, anteras subglobosas, insertas en los senos de los lóbulos de la corola. Estilo de 2 mm

de largo, glabro, globoso en el ápice. Fruto de 5–6 mm de largo por 3–3.5 mm de ancho, obtuso o redondeado en la base, pubérulo, lóbulos del cáliz persistentes, de 1–2 mm de largo, redondeados en el ápice.

Holotipo: CLEMENTE 6908 HAC; Cerro de Cananova, Moa; col.: CLEMENTE, ALAIN y CRISÓGONE, jul. 1949. Isotipo: ALAIN 1010 US, NY.

Ejemplares examinados: CLEMENTE 6205; Cerro de Cananova, Moa, Leg.: CLEMENTE, NESTOR et CRISÓGONE; aug. 1948; HAC, GH, NY; — LEÓN 23032, CLEMENTE 5382; Pinares de Punta Gorda, Moa, Col.: LEÓN, CLEMENTE y NESTOR, 14. 7. 1947. HAC, NY; — HAJB 5965; Playa La Vaca, Moa; Leg.: BISSE et KÖHLER (Fig. 3).

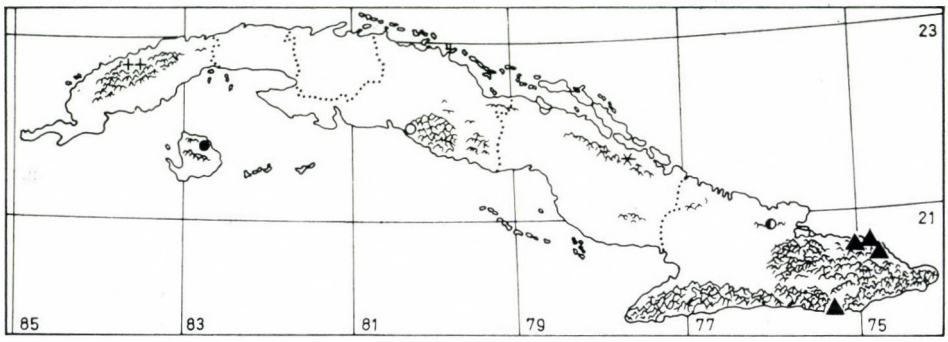

Fig. 3. Distribución de algunas especies del género *Machaonia*, I. — ● *M. Acunae*, + *M. dumosa*, ▲ *M. micrantha*, ○ *M. pubescens*, × *M. tiffina*, △ *M. Urbaniana*, ◐ *M. Urbinoi*;

Esta espécie anteriormente fue incluido en *M. microphylla* Griseb. de la cual se distingue en tener hojas suborbiculares, brillantes, flores mucho mas pequeñas, corolas rosadas, glabras por fuera; plantas mayormente inermes.

Machaonia microphylla Griseb. Mem. Amer. Acad. II. **8:** 510, 1862 (Fig. 4)

(Syn.: *Machaonia variifolia* Urb. Feddes Repert. **19**: 8, 1923)

Arbusto o arbolito de hasta 3–4 m de alto. Ramitas brunneas, escabrosito-hírtulas, las laterales mayormente terminadas en espinas trifurcadas, o divaricadamente trifurcadas. Estípulas anchamente triangulares y deltoideas, aguditas, mucronuladas en las ramas adultas semilunares, obtusas a redondeadas, muy cortas, pelosas. Hojas, aovadas, elípticas, obovadas a oblongo-obovadas, muy variadas en forma y tamaño; obtusas a redondeadas en el ápice, cuneadas en la base, de 4–15 mm de largo por 3–8 mm de ancho. Brillantes en el haz, glabras en ambas caras, con domacias pubérulas en el ángulo de la salida de los nervios laterales 2–3 pares; el limbo cartáceo, plano o frecuentemente involuto hacia el haz.

Inflorescencia en cimas terminales densas, pauci- a multífloras, densamente hirsuto-pelosas. Brácteas lineares, flores sentadas a subsentadas. Cáliz de 3 mm de largo, redondeado en la base, a veces estrechado y obtuso, el tubo de 2 mm de largo, densamente hirsuto, lóbulos 4, de 1 mm de largo, aovados a anchamente lineales, redondeadas en el ápice, hirsutos o a veces glabrescentes. Corola blanca, de 2.5–4 mm de largo, pubérula por fuera, el tubo cilíndrico, de 1.5–2.5 mm de largo, velloso en la garganta y en la parte superior por dentro, glabro en la base, lóbulos 4, obovados u oblongo-obovados, redondeados en el ápice, de 1–1.5 mm de largo,

pelosos a pulverulentos en ambas caras. Estambres 4, filamentos muy cortos o ausentes, anteras inclusas en los senos de los lóbulos de la corola, ovales, mas cortas que los lóbulos. Estilo de 3–3.5 mm de largo, glabro, brevemente bilobulado en el ápice. Fruto oblongo-obovado, obtuso a redondeado en la base, de 2.5–3.5 mm de largo, densamente hirsuto a pubescente, los lóbulos del cáliz persistentes obtusos a redondeados, hirsutos o a veces glabrescentes.

Ejemplares examinados: Cuba; PROV. ORIENTE, Ch. Wright 433; holotypus verificado por A. Borhidi GOET; — PROV. GRANMA: Nagua, in thickets at Rio Yara, Ekman 14161 F, NY, S; — Idem: León 11035 GH, NY, HAC; — Sierra Maestra HAJB 13965; — PROV. HOLGUIN: Preston in dumetis, Ekman 3426 S, NY; — Sierra de Nipe: Rio Piloto en 350 m s. n. m. sobre caliza, Ekman 5782 S; — Holguin, Sabanas arenosas entre Malas Noches y Mir; Areces, Bisse, Gonzalez, Lippold 20999 HAJB. — PROV. SANTIAGO DE CUBA: Sierra Maestra: Loma del Gato, 1100 m. Clemente 6130 NY, HAC; — Tamboril cerca de la Victoria, El Gato; Alain 243 NY; — El Cuero, Britton et Cowell 12727 US, NY; — Sierra de Cobre, Ekman 9239 F, S, US; — Renté, Santiago de Cuba, Clemente 4282 US, HAC; — Idem: Alain 1991 GH, NY, HAC; — Playa Siboney, in coll. calcareis Ekman 8726 S, F; holotypus et isotypus *Machaoniae variifoliae* Urb. — PROV. GUANTÁNAMO: Guantánamo ad flum Yateras, Ekman 10226 S; — Las Ninfas, Guantánamo, Hioram 6751 NY, HAC; — Baitiquiri, Camino al Mina de Yeso, Berazain et Bisse 21853 HAJB; — El Corojo, Montecristo in woods on limestone rocks, León 11810 GH, NY, HAC; — Coastal thickets at Maisi, León 16282 NY, HAC; — Mesa de Lindero Maisi, Alain et López Figueiras 7045 HAC, HAJB; — Meseta de Maisi, Acuña 17397 HAC; — Camino de Caujeri a San Antonio, del Sur, Acuña 17893 HAC; — PROV. MATANZAS: Boca del Rio Canasi sobre caliza Lippold 20457 HAJB.

Discusión: Esta espécie fue entendida por los botánicos en sentido muy amplio por una parte, incluyendo acá las poblaciones que viven en las lomas y serpentinas de la antigua provincia Las Villas y otras mas que viven en los latosoles de serpentinas de Moa. Por otra parte Urban segregó la *M. variifolia*, como espécie distinta, basando su descripción en diferencias encontradas en el tamaño de la corola y del fruto, principalmente. Investigando el material típico de Wright prestado del herbario de Goettingen, encontramos dos ejemplares de *Machaonia* bajo el numero 433 de Ch. Wright. Uno de ellos que lleva la tarjeta: "*Machaonia microphylla* Griseb. Syntypus col.: Ch. Wright Cuba occ. 1863" no es otra, sino el holotipo de *Machaonia pauciflora* Urb. colectada verdaderamente en Cuba Occidental por Wright en 1863; En el mismo ejemplar se encuentran tarjetas originales de Grisebach con su manuscrito y dibujos, que es obviamente la descripción de la *Machaonia microphylla* Griseb. y no concuerda con la planta de la hoja. El otro ejemplar, que lleva la tarjeta siguiente: "*Machaonia microphylla* Griseb. Ch. Wright 433, Prov. Oriente, 1861" sin indicación sobre que ese fuera el tipo, debe considerarse como el tipo auténtico de *Machaonia microphylla* Griseb. Al comparar este ejemplar con el holotipo de *Machaonia variifolia* Urb. encontramos, que no hay ninguna diferencia significativa entre ellos, ni en el habitus, ni en la morfología de las hojas, y de la inflorescencia y flores. Como conclusión de esto tenemos que suprimir esta ultima espécie como válida y ponerla en la sinonimía de *M. microphylla* Griseb.

Ecologia y distribución: *Machaonia microphylla* Griseb. mayormente crece en matorrales áridos y bosques arbustosos secos costeros y subcosteros, mayormente sobre caliza, aunque raramente encontramos algunas poblaciones que viven sobre rocas ácidas, como granita, granodiorita y arena y esta forma tenemos que calificarla como una espécie indiferente en cuanto al contenido de calcio y pH del suelo. La espécie se encuentra sólo dentro del area de la antigua provincia Oriente (salvo un sólo ejemplar de la costa Norte de Matanzas), donde sustituye geográfica- y ecologicamente a *Machaonia havanensis* (Jacq.) Alain como su contrapartida vicariante (Fig. 7).

Tenemos que mencionar, que la especie tiene la distribución mas amplia vertical entre todas la espécies cubanas de este género, creciendo desde 10 hasta 1100 m de altura sobre

el nivel del mar. En estas condiciones tan variadas algunas poblaciones sufren ciertas modificaciones morfológicas sobre todo en cuanto a la pubescencia de y el tamaño del fruto y de las hojas. En la montaña de la Sierra Maestra se encuentran algunas formas menos pubescentes, con fruto mas grande de los que tiene el tipo. Pero estas diferencias se presentan en una forma tan paulatina, que no nos permite diferenciar taxones sobre esta base.

Machaonia minutifolia Britt. et Wils. Mem. Torr. Bot. Club **16:** 112 1920 (Fig. 5)

(Syn.: *Machaonia minutifolia* Alain, Flora de Cuba **5:** 87, 1964 p. p., non *M. minutifolia* Urban Symb. Ant. **9:** 160, 1923)

Arbustos muy ramosos de hasta 2 m de altura, ramitas flexuosas, a menudo inermes, mayormente blanco-grisaceas, diminutamente pelosas a glabrescentes. Estípulas redondeadas, muy cortas, de 0.2–0.3 mm de largo. Hojas obovadas y fasciculadas en las ramas adultas, en las juveniles rómbeas y opuestas, mayormente obtusas redondeadas en el ápice, cuneadas en la base, de 2–4 mm de largo y 1–2 mm de ancho, nervios laterales mayormente ausentes, 1 par en las ramas juveniles, el limbo de la hoja doblado hacia el haz a lo largo del nervio medio, muy brevemente apretado-ciliado en el margen, o glabro, cartáceo.

Flores solitarias sésiles, terminales, o en cimas corto-pedunculadas 3-floras. Cáliz de 1.5 mm de largo, atenuado en la base, glabro, lóbulos de 0.5 mm de largo, aovados a triangulares, obtusos o aguditos, glabros. Corola acampanada de 2 mm de largo, glabra por fuera, ligeramente 4-nervia y 4-angula, lóbulos de 0.5–0.6 mm de largo, agudos, triangulares, con un nervio central, la garganta vellosa por dentro, las demás partes del tubo glabras. Estambres 4, insertos en los ángulos de la corola, muy brevemente filamentados o subsésiles, mas cortos que los lóbulos de la corola, anteras muy pequeñas, suborbiculares u obovadas, de 0.2–0.3 mm de largo. Estilo de 2.5 mm de largo, exserto, acabezuelado en el ápice. Fruto obpiramidal, de 1.5–1.8 mm de largo, 1 mm de ancho arriba, contraido sobre el ovario, abruptamente estrechado en una base obtusa, glabro.

Esta espécies es endémica de las areas serpentinosas de las provincias Camagüey, Villa Clara y Holguin donde crece en los matorrales espinosos y en las sabanas semiantrópicas húmedas de la serpentina (véase: Fig. 7).

Ejemplares examinados: PROV. CAMAGÜEY: Camagüey to Santayana, palm barren. Britton 2397, holotypus! NY; — Santayana, Camagüey, Ekman 15341 S, NY; — Camagüey, sabanas del camino de Cubitas, Acuña y Rodriguez 16325 HAC; — PROV. VILLA CLARA: Santa Clara, palm barren, Britton y Wilson 6130 NY; — Santa Clara in charrascales ásperos, Ekman 18836 S; — Loma Belén near Santa Clara, serpentine barrens, León 14939 GH, NY, HAC; — PROV. HOLGUIN: Loma San Marcos de Aura, vegetación serpentinosa, Areces, Bisse, Gonzalez, Lippold 20774 HAJB.

Machaonia nipensis Borhidi et Fernandez sp. n. (Fig. 6)

(Syn.: *M. minutifolia* Urb. Symb. Ant. **9:** 160, 1923, non Britt. et Wils. Mem. Torr. Bot. Cl. **16:** 112, 1920 — *M. minutifolia* Alain, Flora de Cuba **5:** 87, 1964 p.p.)

Frutex 1–2 m altus, valde ramificatus, ramis plerumque horizontaliter elatis, rariter flexuosis, et depressis, scabroso-pilosis, ramulis lateralibus brevibus in spinis excurrentibus. Spinae simplices, terminales, sicut ramuli ferrugineo-pilosae, postremo glabrae. Stipulae ovatae, 1–1,2 mm longae, apice subulatae, strigosae. Folia opposita, verticillata, brevissime petiolata, petiolis usque ad 0,5 mm longis suffulta, suborbicularia, late ovata vel obovato-elliptica, 1–3 mm longa et 1–2 mm lata, antice rotundata, rariter breviter apiculata, basi rotundata vel subcordata, rariter brevissime cuneata, lamina crasse carnosa, disciformis,

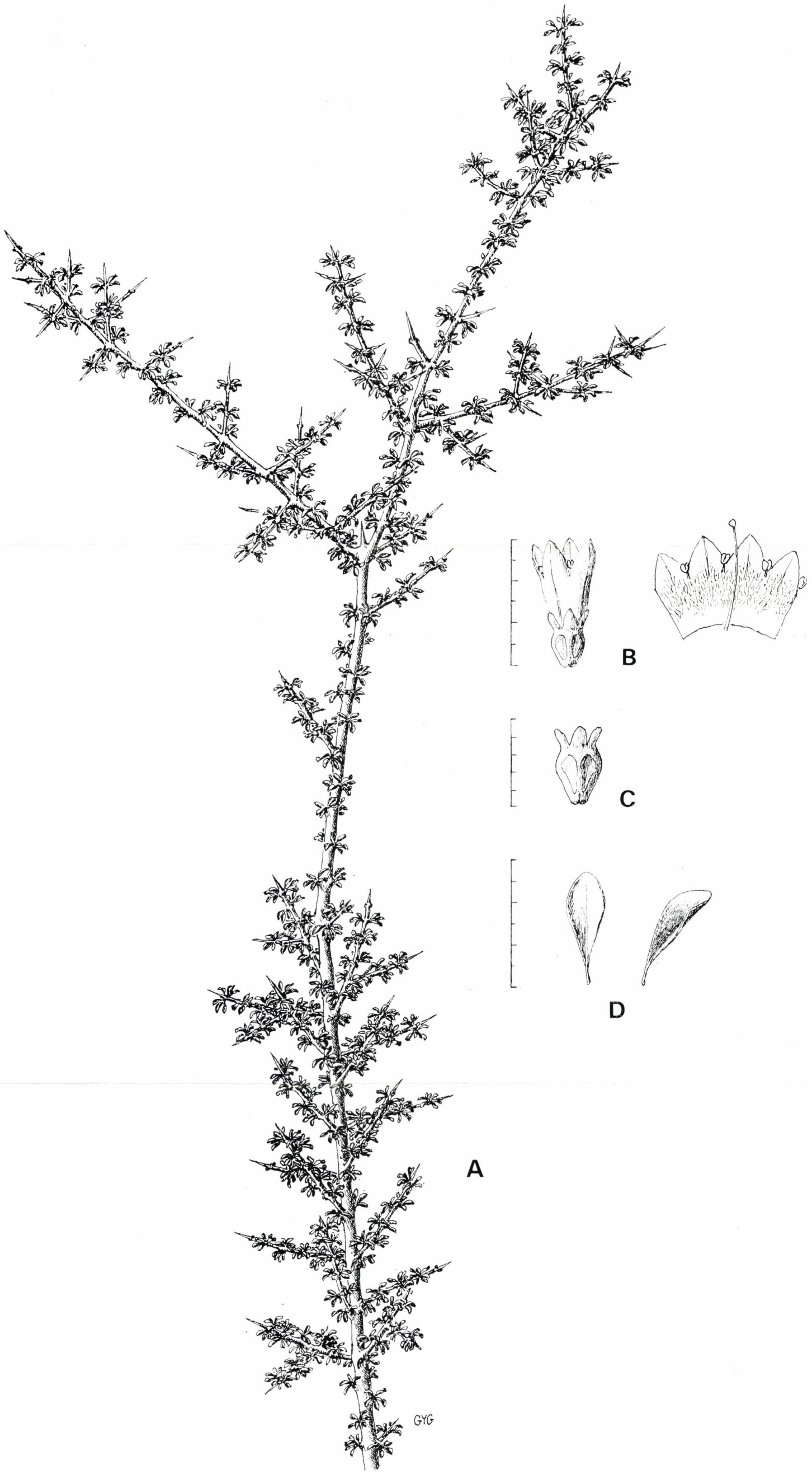

Fig. 5. Machaonia minutifolia Britt. et Wils.; A: Aspecto general; B: Flor y sección de la corola; C: Fruto; D: Hojas. Escalas: 3 y 5 mm. (Dibujo de Gisela Gyurkó)

Fig. 4. Machaonia microphylla Griseb.; A: Aspecto general; B: Flor y corola; C: Frutos D: Hojas. Escala: 5 mm. (Dibujo de Gisela GYURKÓ)

Fig. 8. Machaonia pauciflora Urb.; A: Aspecto general; B: Fruto; C: Hojas. Escala: 5 mm.
(Dibujo de Gisela GYURKÓ)

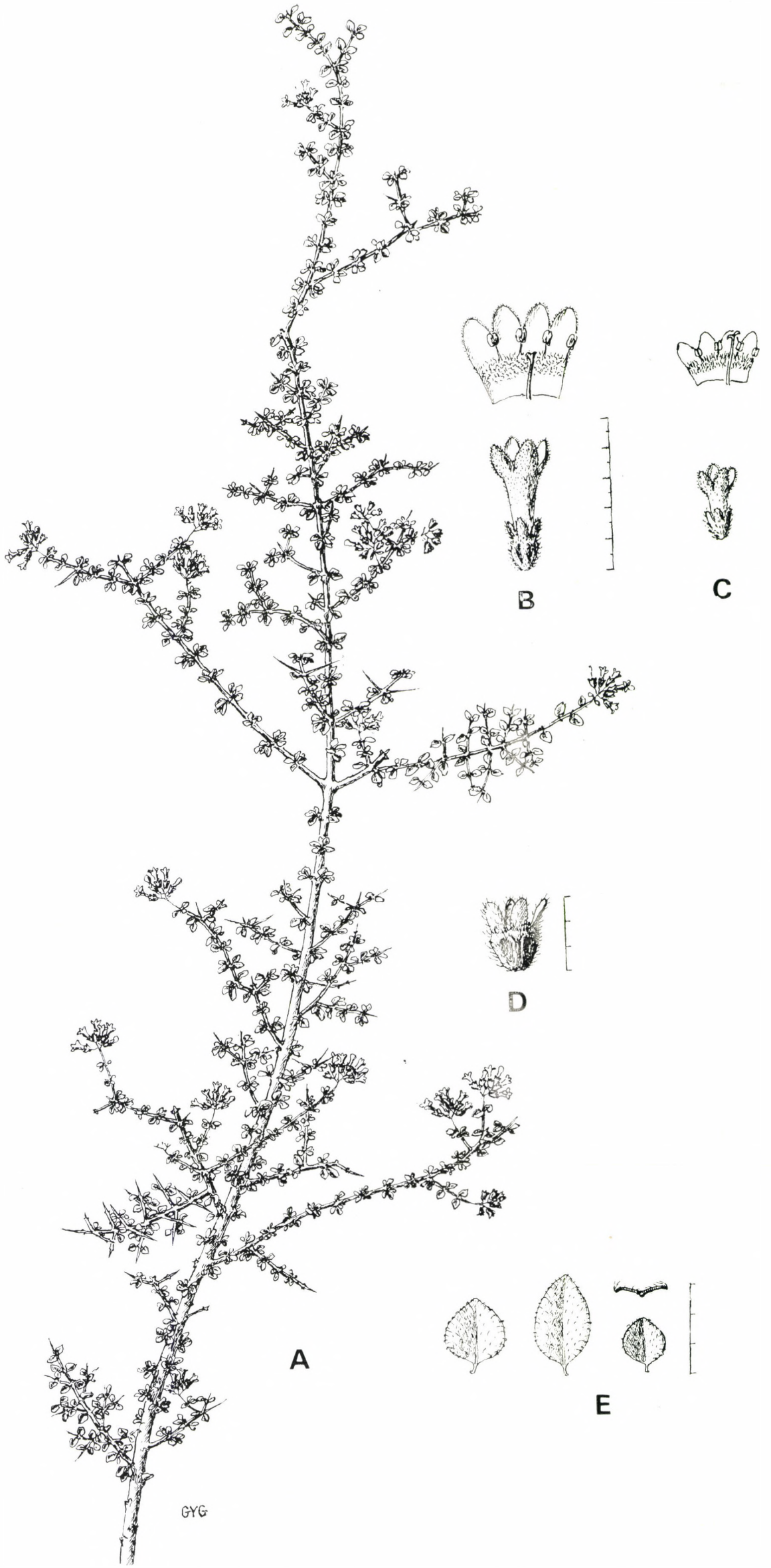

Fig. 6. Machaonia nipensis Borhidi et Fernandez; A: Aspecto general; B: Flor y sección de la corola de la ssp. *nipensis*; C: Flor y sección de la corola de la ssp. *moaensis*; D: Fruto; E: Hojas. Escalas: 5 y 3 mm. (Dibujo de Gisela GYURKÓ)

supra convexa, glabrescens, subtus concaviuscula, glabra, margine incrassata, strigillosa vel glabrescens; nervo medio subtus prominulo, apicem versum leviter impresso et evanescente, lateralibus utrinque nullis. Folia ramorum juvenilium deltoidea, 3–6 mm longa cum nervo laterali utroque latere uno.

Inflorescentiae in ramis lateralibus terminales, racemosae, 1–3-florae. Calyx late obovatus, 2 mm longus, basi rotundatus vel cordatus, tubus calycis 1 mm longus et latus, sparse strigillosus; lobi calycis 4, late ovati, 1 mm longi, apice rotundati, margine strigillosi. Corolla alba, infundibuliformis, 2 mm longus, tubus 2 mm longus, extus glaber basi breviter elatus, fauce attenuatus, intus glaber. Lobi corollae 1 mm longi, ovati, apice rotundati, utrinque dense pulverulenti. Stamina 4, sessilia in sinubus lobulorum corollae, filamenta nulla vel usque ad 0,3 mm longa. Fructus ±3 mm longus et 2,5 mm latus, a lobis calycis persistentibus 1 mm longis coronatus, basi rotundatus vel subcordatus, leviter sulcatus. Semina 2, cylindracea, oblongo-elliptica, brunnea vel brunneo-purpurea, 2–3 mm lata.

Holotypus: 28048 HAC; Cuba; Prov. Holguin (Oriente): Sierra de Nipe; in fruticetis serpentinosis montanis ad Pinares de Mayari, alt. 650 m.s.m. Leg.: A. Borhidi, R. Capote, M. Moncada et R. Ovideo, 5. 9. 1974. Isotypus: BP.

Arbusto de 1–2 m de alto, muy ramificado, con ramas extendidas, a veces flexuosas y decumbentes, escabrositas y densamente espinosas; espinas sencillas de 1–2.5 cm de largo brevemente ferrugineo pelosas, luego glabras. Estípulas interpeciolares aovadas, subuladas en el ápice, 1–1.2 mm de largo, estrigilosas. Hojas opuestas a verticiladas con pecíolo muy corto (hasta 0.5 mm de largo) y glabrescente, el limbo de la hoja suborbicular, anchamente aovado u obovado-eliptico, de 1–3 mm de largo y 1–2 mm de ancho redondeado a obtuso en el ápice a veces apiculado, redondeado a subacorazonado en la base, a veces muy brevemente cuneado, grueso, disciforme y carnoso, convexo en el haz, mayormente glabrescente o con algunos pelos blancos rectos, el margen estrigilosopeloso a glabrescente, el envés algo concavo, glabro; nervio medio prominente en el envés se va estrechando y hundiendo hasta desaparecer antes de llegar al ápice, los laterales nulos en ambas caras. Hojas de las ramitas juveniles deltoideas de 3–6 mm de largo, a veces con 1 par nervios laterales.

Inflorescencias terminales en las ramas laterales, racemosas, 3–5-floras. Cáliz anchamente obovado de 2 mm de largo, redondeado a acorazonado en la base. Tubo del cáliz 1 mm de largo y ancho, escasamente estrigiloso. Lóbulos 4, anchamente aovados de 1 mm de largo, redondeados en el ápice, estrigilosos en el márgen. Corola infundibuliforme de 2 mm de largo, el tubo de 1 mm de largo, glabro en ambas caras, ensanchandose hacia abajo y en la garganta; lóbulos 4, aovados de 1 mm de largo, redondeados en el ápice, densamente pulverulentos en ambas caras. Estambres 4, sésiles en los sénos de los lóbulos de la corola, filamentos nulos o hasta de 0.3 mm de largo. Fruto anchamente obovado de 3 mm de largo y 2.5 mm de ancho, lóbulos del cáliz pesistentes aovados, de 1 mm de largo, redondeado o acorazonado en la base, longitudinalmente surcado. Semillas 2, cilíndricas a oblongo-elípticas, pardas a pardo-rojizas de 2.5–3 mm de largo y 1–1.2 mm de ancho.

Holotipo: 28048 HAC; Cuba; Prov. Holguin (Oriente); Sierra de Nipe. En los charrascales montanos de Pinares de Mayari. Col.: A. Borhidi, R. Capote, M. Moncada et R. Ovideo, 5. 9. 1974.

Ejemplares examinados: Sierra de Nipe: Falda Norte de la Loma Mensura, Borhidi y Muñiz 27922 HAC, BP. — In pinetis ad Loma Mensura cca 725 m. Ekman 9723 S, GH, F, US, 9724 S. — Loma Mensura, Shafer 3791 NY; — Ibidem: Ekman 5756 S; — Ibidem:

BORHIDI et MUÑIZ 27923 HAC; — Ibidem: BISSE et ROJAS 3872 HAJB; — Ibidem: BISSE 15782 HAJB; — Ibidem: LÓPEZ FIGUEIRAS 1762 HAJB, HAC; — Ibidem: LÓPEZ FIGUEIRAS 1093 HAJB, HAC; — Ibidem: ALAIN, ACUÑA et RAMOS 7919, 7986, 8127; HAC, HAJB; — Sierra de Nipe: Rio Piloto in charrascales, 350 m. EKMAN 15054 F, S; — Ibidem: EKMAN 2522, 2318; — Cabezadas del Rio Piloto BORHIDI, CAPOTE et OVIEDO, 10. 9. 1974. HAC, BP. — Pinares pedregosos cerca del Campamento de la AC, Pinares de Mayari, leg.: BORHIDI 6. 9. 1974. HAC, BP; — Sierra de Nipe: Cayo La Plancha, LEÓN et ALAIN 19107 HAC; — Ibidem: HOWARD 6165 GH; — Sierra de Nipe: San José, leg.: LEÓN, CLEMENTE et HOWARD 20352 NY, HAC; — Cayo Sabinal, Sierra de Nipe, Pinares de Mayari, leg.: ALAIN, ACUÑA et RAMOS 7919 HAC; — Loma del Winch, La Caridad, Mayari, leg.: ALAIN, ACUÑA et RAMOS 8076 HAC; — Sierra del Cristal HAJB 30710.

ssp. **moaensis** Borhidi et Fernandez ssp. nova

A typo differt foliis glabris, ferrugineis in sicco, calyce 1–1,2 mm longo, lobis acutiusculis, corolla rosada vel purpurea, 1,5–2,5 mm longa.

Holotypus: CLEMENTE 4027 HAC; Cuba; Prov. Holguin (Oriente); Rio Jaragua, Cayoguán, Moa. Leg.: CLEMENTE et ALAIN, 21. 7. 1944. Isotypi: GH, NY, US.

Difiere del tipo en tener hojas glabras, rojizas cuando secas, cáliz de 1–1.2 mm de largo con lóbulos aguditos a obtusos, corola rosada a roja, de 1.5–2.5 mm de largo.

Holotipo: CLEMENTE 4027 HAC; Cuba; Prov. Holguin (Oriente); Rio Jaragua, Cayoguán, Moa. Leg.: CLEMENTE et ALAIN, 21. 7. 1944. Isotypos: GH, NY, US.

Ejemplares examinados: PROV. HOLGUIN: 15 kms SW of the sawmill at Moa. HOWARD 6165 GH; — Playa de la Vaca, Moa; MARIE-VICTORIN y CLEMENTE 5698 GH, HAC; — Pine barren, Rio Yagrumaje, Moa; MARIE-VICTORIN, CLEMENTE y ALAIN 21796 NY, HAC; — Moa, Cayo Probado, orillas de las cabezadas del Rio Jaguani, BISSE y BERAZAIN 3. 4. 1972. HAJB; — La Melba, Valle del Arroyo Grande en la falda sur de la Sierra de Moa; BISSE y LIPPOLD 11115 HAJB. — PROV. GUANTÁNAMO: Palenque, Cuchillas de Toa, Cayo Fortuna a lo largo del rio Toa; BISSE 16910; — Peña Prieta, La Magdalena, Toa, alt. aprox. 600 m; ALAIN 3134 NY, HAC.

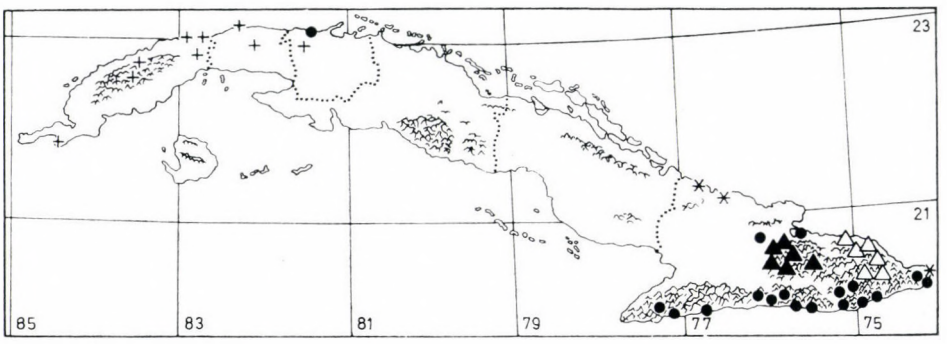

Fig. 7. Distribución de algunas especies del género *Machaonia*, II. — + *Machaonia havanensis* ssp. *havanensis*, * *M. havanensis* ssp. *orientalis*, ● *M. microphylla*, ▲ *M nipensis* ssp. *nipensis*, △ *M. nipensis* ssp. *moaensis*

Machaonia nipensis Borhidi et Fernandez es una espécie ampliamente colectada por los botánicos. Todos los ejemplares fueron determinadas como *M. minutifolia* Britt. y Wils. en base a una identificación erronea de URBAN, provocada por la descripción incompleta de esta ultima espécie, y por la condición, que URBAN no tuvo acceso para investigar el ejemplar tipico colectado por BRITTON en Santayana (Camagüey). (Véase: Urban Symb. Ant. *9*: 160, 1923.) *Machaonia nipensis* se distingue en tener hojas suborbiculares, coriáceas, carnosas, cáliz semiorbicular, peloso y corola pelosita por fuera con lóbulos redondeados. Las 2 subespécies diferenciadas por nosotros tienen caracteres por lo común cuantitativamente diferentes y areas geográficamente bien separadas (véase: Fig. 7).

Machaonia pauciflora Urb. Symb. Ant. **5:** 512, 1908 (Fig. 8)

(Syn.: *Machaonia trifurcata* Urb. Symb. Ant. **5:** 512, 1908; *Machaonia littoralis* Britt. Bull. Torr. Bot. Club **43:** 453, 1916)

Arbustos o arbolitos de hasta 3–4 m de alto, ramitas brevemente pelosas, las adultas glabras, terminadas en espinas sencillas o trifurcadas, a veces inermes. Estípulas triangulares, de 0.3–0.5 mm de largo, terminadas en un mucrón de 0.2–0.5 mm de largo, a menudo caedizo. Hojas elípticas, obovadas a rómbico-obovadas, a veces aovadas, opuestas, con pecíolos de 0.5–2 mm de largo, muy variables, redondeadas a obtusas en el ápice, cuneadas o atenuadas en la base, de 0.6–1.5 cm de largo por 0.4–1 cm de ancho, nervios laterales 2–3 pares visibles en el haz, ligeramente hundidos en el envés, a veces inconspicuos u obsoletos; el limbo cartáceo a subcoriáceo, el margen plano, glabro a diminutamente pubérulo en el nervio medio del envés, sin domácias.

Inflorescencia corimbosa o corimboso-cimosa, pauci- a multíflora, el cáliz de 1.3–2 mm de largo, el tubo deprimido pubérulo a glabrescente o esparcidamente peloso, lóbulos aovados a triangulares, de 0.5–1 mm de largo, atenuados en el ápice obtuso, pelosos en el margen o completamente glabros. Corola de 1.5–3 mm de largo, glabra por fuera, el tubo y la garganta vellosos por dentro. Estambres 4, insertos en los ángulos de la corola con filamentos muy breves, mas cortos que los lóbulos de la corola, anteras pequeñas, suborbiculares, de 0.2–0.4 mm de largo, estilo de 1–1.5 mm de largo inserto en la corola, glabro. Fruto obovado u oblongo-obovado de 4–4.5 mm de largo, redondeado a obtuso en la base, ligeramente pelosito a glabro, lóbulos del cáliz de 0.5–1 mm de largo, pelosos a glabros.

ssp. **pauciflora**

(Syn.: *Machaonia littoralis* Britt. Bull. Torr. Bot. Club **43:** 453, 1916)

Se distingue en tener hojas glabras, diminutamente reticuladas en el envés, coriáceas, tubo del cáliz y fruto glabro.

Ejemplares examinados: WRIGHT 433 Cuba occ. 1863; holotypus GOET; isotypos: NY, HAC, S, Herb. Jimeno; — ISLA DE PINOS: Siguanea BRITTON, BRITTON y WILSON 14942 NY, US (holotypo e isotypo de *Machaonia littoralis* Britt.); — Isla de Pinos: Westport region, white sand savanas, KILLIP 45501 US, HAC; — Isla de Pinos, BLAIN 44, F 78999; — Isla de Pinos: Siguanea, BRITTON, BRITTON y WILSON 14943; — Isla de Pinos, Loma Daguilla, EKMAN 12487 S; — Isla de Pinos, arenas blaucas cerca de las Delicias, BISSE 19418 HAJB; — Sabana arenosa cerca del Hotel Colony, BISSE y LIPPOLD 12125, febr. 1969. HAJB; — Isla de Pinos, Clara del Piñal, mai. 1967. HAC. 26710

ssp. **trifurcata** (Urb.) Borhidi et Fernandez comb. et status novus

(Basionymon: *Machaonia trifurcata* Urb. Symb. Ant. **5:** 512, 1908. Syn.: *Machaonia cymosa* Griseb. Cat. Plant. Cub. 1866: 139, non Griseb. Flora Brit. West. Ind. 1961: 348)

Difiere del tipo en tener ramitas mayormente espinosas, hipantio y cáliz deprimido-peloso, lóbulos del cáliz ciliados.

Ejemplares examinados: Cuba, Ch. WRIGHT 2760 GOET, holotipo, isotipos, S, GH, US, HAC; — WRIGHT 433 p. p. S, MICH; — PROV. PINAR DEL RIO, Toscano, EKMAN 17673 F, NY, S, HAC; — Pinar del Rio, Rangel, Loma Zambumbia, alt. 500 m LEÓN 12630 GH, NY, HAC; — Sierra del Rosario, Rio La Planta, Rangel alt. 500 m ALAIN 531 NY; — La Cajalbana, Consolación del Norte, ROIG 4555 HAC; — Ibidem: ACUÑA y ROIG 9091 HAC; — Ibidem: ACUÑA 16423 HAC; — Bahia Honda, Las Pozas, ALVAREZ, ARECES, BISSE, KÖHLER 32669 HAJB; — Ibidem: Toscano, ACUÑA 17053; — Los Palacios, Central de La Francia, ACUÑA 15630; — Sierra de los Organos, Mogote El Mural, Viñales, BORHIDI 13798 HAC, BP; — Ibidem: M. MONCADA 27855 HAC; — Sierra de La Güira, pinares, DEL-RISCO 27221 HAC; —Pinar del Rio, 10573 HAJB;—ROIG 9185, HAC; Toscano, La Palma; — Mantua, BORHIDI, R. CAPOTE 28307 HAC;—PROV. CAMAGÜEY: Guaimaro, Camagüey suelo arenoso, ARECES, BISSE, LIPPOLD 31483 HAJB.

ssp. **glabrata** Borhidi et Fernandez ssp. nova

A typo differt: foliis supra opacis, membranaceis vel charataceis, nervis lateralibus non prominulis, calycis 1,2–1,5 mm longis, glabris, corolla 1,4–2 mm longa, staminibus sessilibus, fructibus basi longiore attenuatis.

Holotypus: Isla de Pinos: Loma Bibijagua, ARECES, BISSE, KÖHLER, DIAZ, GUTIERREZ 32727 HAJB; Isotypi: HAC, BP.

Difiere del tipo en tener hojas membranaceas a cartáceas, mates en el haz, con nervios laterales no prominulos, caliz y corola muy pequeña, ramitas con espinas trifurcadas, pulverulentas.

Holotipo: Isla de Pinos, Lomas Bibijagua al lado de la Playa Bibijagua. Col.: ARECES, BISSE, KÖHLER, DIAZ, GUTIERREZ, 32727 HAJB. Isotipos: HAC, BP; —

Ejemplares examinados: ACUÑA 19949 HAC; Pinar del Rio: Peninsula de Guanahacabibes, Tetas de Maria la Gorda; — Sierra de Viñales, in rough limestone rocks, EKMAN 16581 F, S.

Discusión: Al estudiar el material muy variable de las poblaciones existentes en Cuba occidental surgen cada vez mas dificultades en diferenciar los ejemplares de *Machaonia pauciflora* y *M. trifurcata* Urb. *Machaonia pauciflora* Urb. es una forma bastante extrema de un complejo rico en formas, además esta espécie fue descrita en fruto, mientras *Machaonia trifurcata* en estado de floración, condición que no facilita la comparación objetiva de los dos taxa. La descripción de *Machaonia pauciflora* está basada principalmente en la forma y pelosidad del fruto, caracteres que desde la época de la floración hasta la madurez completa sufren cambios notables. Además se observó, que entre la pelosidad del hipantio, de los lóbulos del cáliz y el tamaño de los lóbulos no hay concordancia consecuente. Llegamos a la conclusión que las poblaciones colectadas en las arenas blancas de Isla de Pinos tienen la mayor semejanza con la WRIGHT 433; y las consideramos como *Machaonia pauciflora* Urb. tipica. Al tipo de la *Machaonia trifurcata* Urb. lc corresponden los otros ejemplares colectados en las pizarras y suelos de mocarrero de Pinar del Rio, pero al mismo tiempo encontramos poblaciones que viven en las serpentinas de Pinar del Rio y representan una serie de formas intermediarias entre los dos taxa.

Fig. 10. Machaonia pubescens Borhidi et Fernandez; A: Aspecto general; B: Flor y sección de la corola; C: Hojas. Escalas: 3 y 5 mm. (Dibujo de Gisela GYURKÓ)

Por esta razón consideramos, que *Machaonia trifurcata* Urb. no puede mantenerse como especie distinta, sino una subespécie que tiene distribución geográfica distinta creciendo en las pizarras, serpentinas y mogotes de Pinar del Rio, mientras *M. pauciflora* ssp. *pauciflora* es una endémica de Isla de Pinos. En las areas costeras y subcosteras calizas se presentó otro taxon de este complejo, el que consideramos como una tercera subespécie de el *Machaonia pauciflora* Urb. nominandola ssp. *glabrata*, que se encuentra en las costas calizas de Pinar del Rio e Isla de Pinos igual (véase: Fig. 9).

Aunque el taxon mas corriente entre los tres es la ssp. *trifurcata* (Urb.) Borhidi et Fernandez, tenemos que mantener el nombre especifico de *M. pauciflora* Urb. que fue publicado en la misma página de Symbolae Antillanae, pero con antelación.

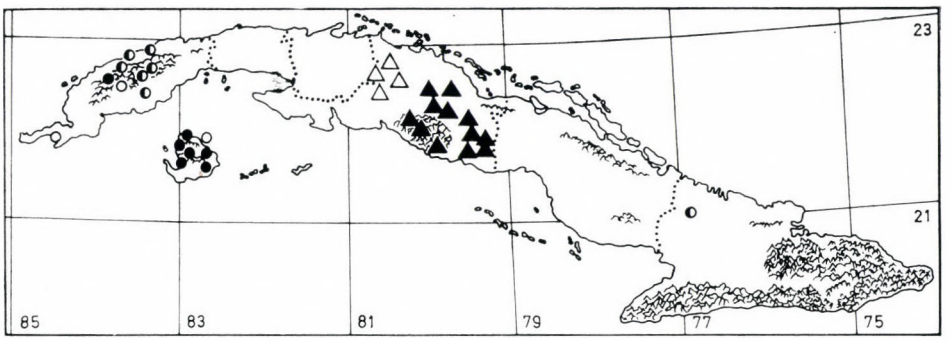

Fig. 9. Distribución de algunas espécies del género *Machaonia*, III. — ● *M. pauciflora* ssp. *pauciflora*, ○ *M. pauciflora* ssp. *glabrata*, ◐ *M. pauciflora* ssp. *trifurcata*, △ *M. subinermis*; ssp. *subinermis*, ▲ *M. subinermis* ssp. *armata*

Machaonia pubescens Borhidi et Fernandez sp. n. (Fig. 10)

(Syn.: *Machaonia microphylla* Howard, Briggs et al. in Exsicc. Plant. Gray. 1480 non Griseb.)

Frutex usque ad 3,5–4 m altus, subinermis. Rami hornotini subteretes, ferruginei, pilis, rigidis patentibus albis dense hirsuti, rariter in spinas tenues, 5–6 mm longas excurrentes, veteriores teretes, albi. Stipulae triangulares, 0,2–0,5 mm longae, apice mucronatae, dense hirsutae. Folia opposita vel in nodis ramorum veteriorum fasciculata, usque ad 1 mm longe petiolata, elliptica vel ovata, apice rotundata vel apiculata et obtusa, basi breviter vel longe cuneata, 1–2 cm longa et 0,5–1,3 cm lata, nervo medio supra leviter impresso, subtus valde prominente, lateralibus utroque latere 2–3, supra obsoletis vel tenuissime prominentibus, subtus prominulis; lamina utrinque pilis brevibusque mollibus satis dense pubescens et subtus in nervis strigilloso-hirsuta, membranacea vel subchartacea.

Inflorescentiae terminales, dense racemosae, multiflorae, hirsutae. Flores subsessiles. Calyx obovatus, 1,5–1,8 mm longus, basi rotundatus, lobi usque ad 1 mm longi, semiorbiculares, apice rotundati, cum tubo densissime albo-hirsuti. Corolla alba, fragrans, late infundibuliformis, 1,5–2 mm longus, extus pubescens. Tubus 1,5 mm longus, extus puberulus, intus in fauce villosus, basi puberulus; lobi 4, triangulares, obtusae, extus pubescentes, intus puberuli, 0,5 mm longi. Stamina 4, in sinubus corollae sessiles vel subsessiles. Stylus 1,5 mm longus, apice capitatus. Fructus non visus.

Holotypus: Plantae Exsiccatae Grayanae 1480, in HAC: Cuba; Prov. Cienfuegos; dry open hillside on limestone, 350 m a. s. l., near Rio San Juan at Camino del Sur. Leg.: HOWARD, BRIGGS et al. 17. 7. 1951. Isotypi: US, GH, NY.

Arbusto de hasta 3.5–4m de alto, subinerme. Ramitas jóvenes subcilíndricas, ferrugineas, densamente hirsutas con pelos rígidos, blancos, raramente espinosas con espinas de 5–6 mm de largo, ramas adultas, cilíndricas, blancas. Estípulas triangulares, de 0.2–0.5 mm de largo, mucronadas en el ápice, densamente hirsutas. Hojas opuestas o fasciculadas en los nodulos de las ramas adultas, con pecíolo de hasta 1 mm de largo, elípticas o aovadas, redondeadas o apiculadas en la base, breve- o largamente cuneadas en la base, de 1–2 cm de largo por 0.5–1.3 cm de ancho; nervio medio hundido en el haz, muy prominente en el envés, los laterales 2–3 pares obsoletos en el haz o poco promínulos y prominentes en el envés; el limbo membranaceo a subcartáceo, densamente pubescente en ambas caras, y estrigilloso-hirsuto en los nervios del envés.

Inflorescencias terminales, densamente racemosas, hirsutas, multífloras. Flores subsentadas. Cáliz obovado, de 1.5–1.8 mm de largo, redondeado en la base, lóbulos 4, semiorbiculares, de hasta 1 mm de largo, redondeados en el ápice, con el hipantio muy densamente hirsutos. Corola blanca, aromática, anchamente embudada, de 1.5–2 mm de largo, pubescente por fuera. El tubo de 1.5 mm de largo, pubérulo por fuera, vellosa en la garganta, pubérula por dentro en la base; lóbulos 4, triangulares obtusos, pubescentes por fuera, pubérulos por dentro, de 0.5 mm de largo. Estambres 4, anteras sentadas en los senos de los lóbulos de la corola. Estilo de 1.5 mm de largo, cabezuelado en el ápice. Fruto no visto.

Holotipo: Plantae Exsiccatae Grayanae 1480, en HAC!; Cuba; Prov. Cienfuegos, en pendientes áridos colinosos sobre caliza en alt. aprox. 350 m s. n. m., cerca del Camino del Sur de Rio San Juan. Col.: HOWARD, BRIGGS y otros, 17. 7. 1951. Isotipos: US, GH, NY.

Esta espécie fue clasificada cómo *M. microphylla* Griseb. de la cuál se distingue en tener hojas membranáceas o subcartáceas más grandes, densamente pubescentes en ambas caras, corola más pequeña, lóbulos del cáliz semiorbiculares. Conocida sólo de la colecta típica. Endémica (véase: Fig. 3).

Machaonia subinermis Urb. Symb. Ant. **9:** 530, 1928 (Figs 11–12)

(Syn.: *Machaonia microphylla* auct. cub. et amer. quoad plantae in Prov. Las Villas lectae, non GRISEB.)

Arbustos o arbolitos, de hasta 2–3 m de alto. Ramitas grisáceas a brunneas, los laterales alargadas, inermes, subespinescentes a ramificado-espinosas, las jóvenes diminutamente pelosas. Estípulas pequeñas, triangulares, brevemente connadas en la base, a veces formando un anillo muy breve, truncado. Hojas de hasta 1 mm de largo, pecioladas, polimorfas, las de las jóvenes estériles aovadas a aovado-orbiculares o subtriangulares, a menudo anchamente rómbeas, las de las ramas adultas, fértiles, lineal-obovadas, obovado-oblongas u oblongo-elipticas, fasciculadas en los nudos, de 5–10 mm de largo por 1–7 mm de ancho, mayormente glabras y brillantes en ambas caras, cartáceas a subcoriáceas. Nervios laterales 1–3 pares, ligeramente hundidos en el envés, domacias ausentes.

Inflorescencias terminales, paucífloras, ligeramente acabezueladas, a cimosas o cimoso-umbeladas. Flores sentadas a subsentadas con un pedicelo de hasta de 0.5 mm de largo. Tubo

del cáliz obovado-orbicular de 1 mm de largo, diminutamente deprimido-peloso; lóbulos 4, igual o poco mas largos que el tubo, estrechamente aovados, obtusos a redondeados en ápice, glabros o a veces ciliados en el márgen, de 1.3 mm de largo. Corola blanca, de 2.5–3 mm de largo, brevemente pelosa por fuera, el tubo de 1.5–2 mm de largo, ensanchado hacía arriba, pubescente por dentro, la garganta glabra. Lóbulos de la corola de 1–1.5 mm de largo, oblongo-aovados obtusos a redondeados, glabros en ambas caras. Estambres insertos en los ángulos de los lóbulos de la corola, más cortos que los lóbulos, filamentos muy breves; anteras cuadrangular-orbiculares. Estilo de 1.5 mm de largo, glabro, brevemente bifido en el ápice. Fruto obovado a brevemente obovado, redondeado en la base, de 3–4 mm de largo y 2.5 mm de ancho, diminutamente pubérulo.

ssp. **subinermis** (Fig. 11)

Se caracteriza en tener ramitas alargadas, inermes, hojas lineal-oblongas a lineal-obovadas, fasciculadas en las ramas, flores y frutos glabrescentes.

ssp. **armata** Borhidi et Fernandez ssp. nova (Fig. 12)

A typo differt: ramis lateralibus spinosis trifurcatis vel bifidi-trifurcatis, foliis ellipticis vel rhombeis, calycis hypanthiisque densiter patenterque pilosis.

Holotypus: León et Clemente 6658; Cuba; Sierra Sancti Spiritus, Sabana del Tibisial, 1–11. 8. 1916. HAC. Isotypi: US, NY.

Difiere del tipo en tener ramitas laterales espinosas, terminadas en espinas trifurcadas o bifidamente trifurcadas, hojas elipticas o rómbeas, cáliz e hipantio mas pubérulo con pelos extendidos.

Holotipo: León y Clemente 6658; Cuba; Sierra de Sancti Spiritus, Sabana del Tibisial, col.: León y Clemente 1–11. 8. 1916. HAC; isotipos: US, NY.

Ejemplares examinados:

ssp. **subinermis:** Cuba; PROV. VILLA CLARA; Motembo in slightly wet savannas, Ekman 16809 S Holotypus; Isotypi: F, US. — Idem: León et Loustalot 9356 GH, NY, HAC. — Prov. Villa Clara: Sabana arenosa, Manacas, Bisse y Rojas 4398 HAJB; — Idem: Acuña y Correl 18661 HAC; — Villa Clara: Sabanas de Cascajal, Acuña 14789 HAC.

ssp. **armata:** PROV. VILLA CLARA: Sierra de Agabama, Sur de Santa Clara, Alain 3966 GH, HAC; — Prov. Villa Clara: Palm barrens about 6 km West of Santa Clara, L. B. Smith, Hogdon et al. 3158 F, GH, NY, S, US; — Villa Clara: Sabana near to Santa Clara, León 14961 HAC, NY; — Palm barren Santa Clara, on serpentine, Ekman 14057 S; — Prov. Villa Clara; cuabales entre Santa Clara y Falcón, Bisse y Rojas 4726 HAJB; — PROV. CIENFUEGOS: Sierra de Trinidad: San Blas Buenos Aires, Gaviñas- Howard 6537 GH, NY; — PROV. SANCTI SPIRITUS: Sierra de Sancti Spiritus; Sabana del Tibisial, León et Clemente 6658 HAC holotypus, US y NY isotipi. — Idem: León et Roca 8081 US, NY; — Lomas de Banao, Luna 833 HAC, NY; — Sierra Sancti Spiritus: Loma Ponciano, León et Clemente 6708 NY, HAC; — Sierra de Escambray: Loma del Burro, Bisse et Rojas 4726 HAJB; — Idem: Areces et Berazain 25120 HAJB; — Prov. Sancti Spiritus: Serpentinas de la Jíquima, al Norte de Minas de Jarahueca, 35279 HAJB.

Discusión: Los ejemplares espinosos de esta espécie — con pocas excepciones — fueron determinados como *M. microphylla* Griseb. Un estudio cuidadoso de la estructura floral y del

fruto nos convenció, que todas las poblaciones de las lomas mas altas y de las areas secas serpentinosas de la antigua provincia Las Villas pertenecen a *Machaonia subinermis* Urb. representando una subespécie, que vive en condiciones ecológicas diferentes de las del tipo, y en una area geográfica distinta. Las poblaciones del tipo crecen en suelos de mocarrero, inundados periodicamente, o en sabanas húmedas serpentinosas, representando una forma indudablemente extrema de esta espécie. *M. subinermis* es una espécie vicariante de *M. microphylla* Griseb. la que sustituye en todas las situaciones ecológicas convenientes de la parte central y meridional de la antigua provincia Las Villas. En cuanto a la forma y pelosidad del cáliz, hipantio y frutos las dos espécies aqui mencionadas son muy semejantes, pero facilita su distinción la presencia o ausencia de las domacias en las hojas, caracter que permite su clasificación también en estado estéril.

Analizando la distribución de las dos subespécies de *Machaonia subinermis*, encontramos, que la ssp. *subinermis* se encuentra en las zonas de mocarrero de Cascajal y Manacas y en las serpentinas que estan al Oeste de Santa Clara. La ssp. *armata* crece en las zonas serpentinosas al Este y Sur de Santa Clara y principalmente en las Sierras de Trinidad y Sancti Spiritus (véase: Fig. 9).

Machaonia tiffina Urb. Symb. Ant. **9:** 531, 1928 (Fig. 13)

Arbusto. Ramitas cilíndricas, las adultas grisaceas, mayormente inermes, alargadas, las jóvenes diminutamente pubérulas. Estípulas minutas de 0.2–0.3 mm de largo, triangulares. Hojas con pecíolos muy cortos de 0.3–0.8 mm de largo, obovadas, cuneadas en la base, obtusas a redondeadas en el ápice, de 3–6 mm de largo y 2–4 mm de ancho, nervio medio poco promínulo en el haz, prominente en el envés, rojizo, los laterales 1–2 pares visible en el envés, el limbo plano membranáceo a subcartáceo.

Flores muy pocas, terminales, mayormente agrupadas en cimas 3-floras; pedicelos de 0.5 mm de largo; cáliz muy pequeño, de 1.3–1.5 mm de largo, el tubo obovado, glabro, de 0.8–1 mm de largo, redondeado en la base, los lóbulos de 0.4–0.7 mm de largo, glabros. Corola 3–3.5 mm de largo, el tubo poco ampliado arriba, lóbulos 4, de 1.5–1.7 mm de largo, oblongo-obovados, redondeados en el ápice, reticulado-nerviados. Estambres insertos en los ángulos de los lóbulos de la corola, filamentos de hasta 0.5 mm de largo, anteras anchamente elípticas a obovadas a suborbiculares. La garganta de la corola vellosa por dentro, el tubo glabro por fuera, los lóbulos glabros en ambas caras. Estilo de 1.3–1.5 mm de largo, muy brevemente bífido en el ápice. Fruto obovado, redondeado en la base, de 2.5–3.0 mm de largo, glabro, lóbulos del cáliz persistentes aovados, obtusos, de 0.7–1 mm de largo, glabros.

Ejemplares examinados: Cuba; Prov. Camagüey, prope Tiffin, in pratis. EKMAN 15399 S, holotypus!, isotypus: F.

Conocida sólo de la colecta tipica. Indudablemente es una espécie válida, buena, que se distingue por carácteres buenos de la espécie proxima, *M. minutifolia* Britt. et Wils., que crece en la misma area (véase: Fig. 3).

Machaonia urbaniana Standley North Amer. Fl. **32:** 222, 1934 (Fig. 14)

Arbusto muy densamente ramificado, con ramitas cilíndricas, brunneas a grisáceas, con internodios muy cortos, ramitas laterales breves, terminadas en espinas rígidas mayormente trifurcadas o bifidamente trifurcadas de hasta 1.5 cm de largo, las jóvenes densamente pubescentes. Estípulas en forma de anillo, muy cortas, truncadas en el ápice. Hojas opuestas, cartáceas, subsentadas con pecíolos de 0.4–0.8 mm de largo, oblongo-obovadas, oblongo-

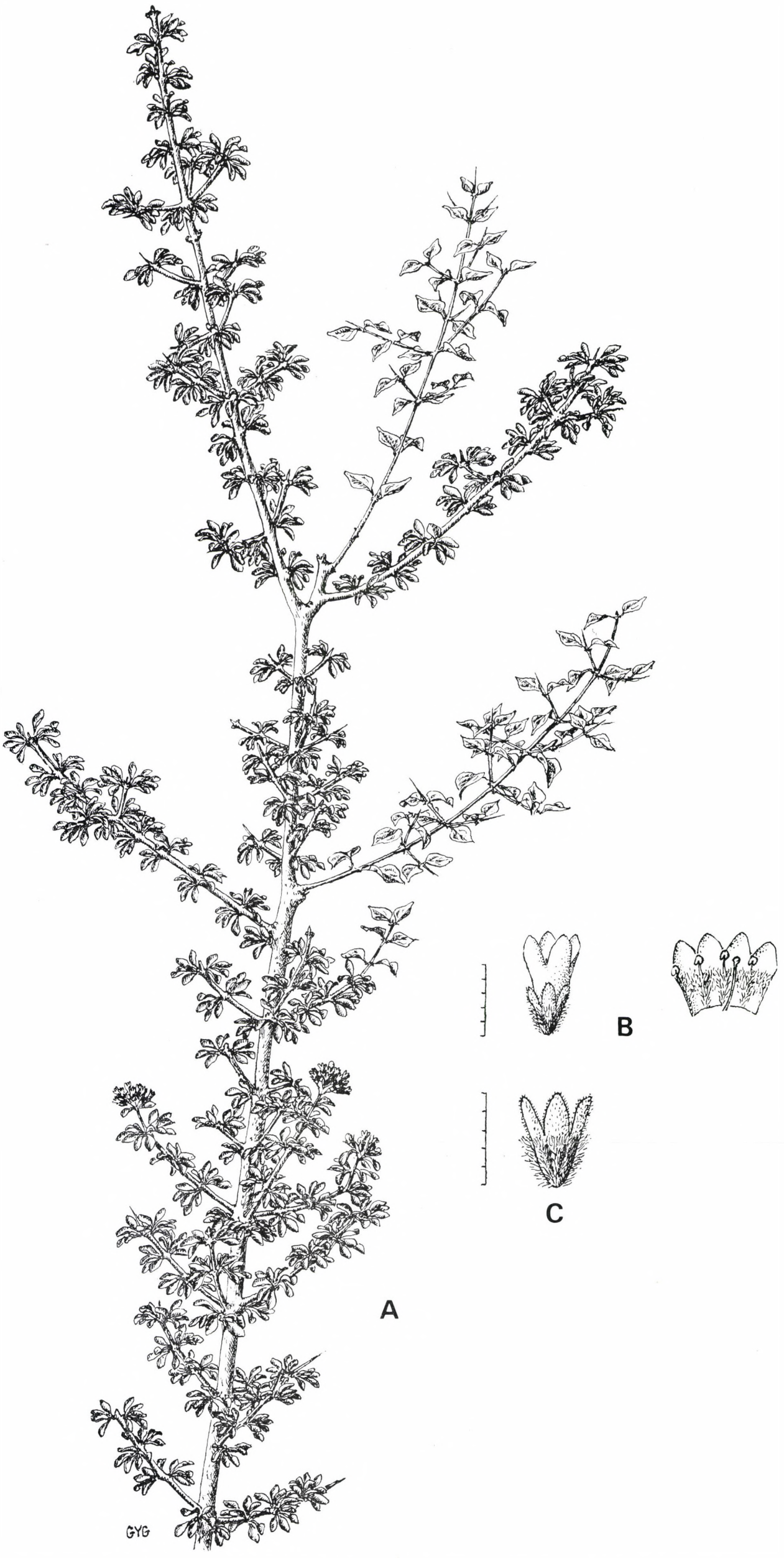

Fig. 11. Machaonia subinermis Urb.; A: Aspecto general; B: Flor y sección de la corola. C: Cáliz frutifero. Escala: 5 mm. (Dibujo de Gisela GYURKÓ)

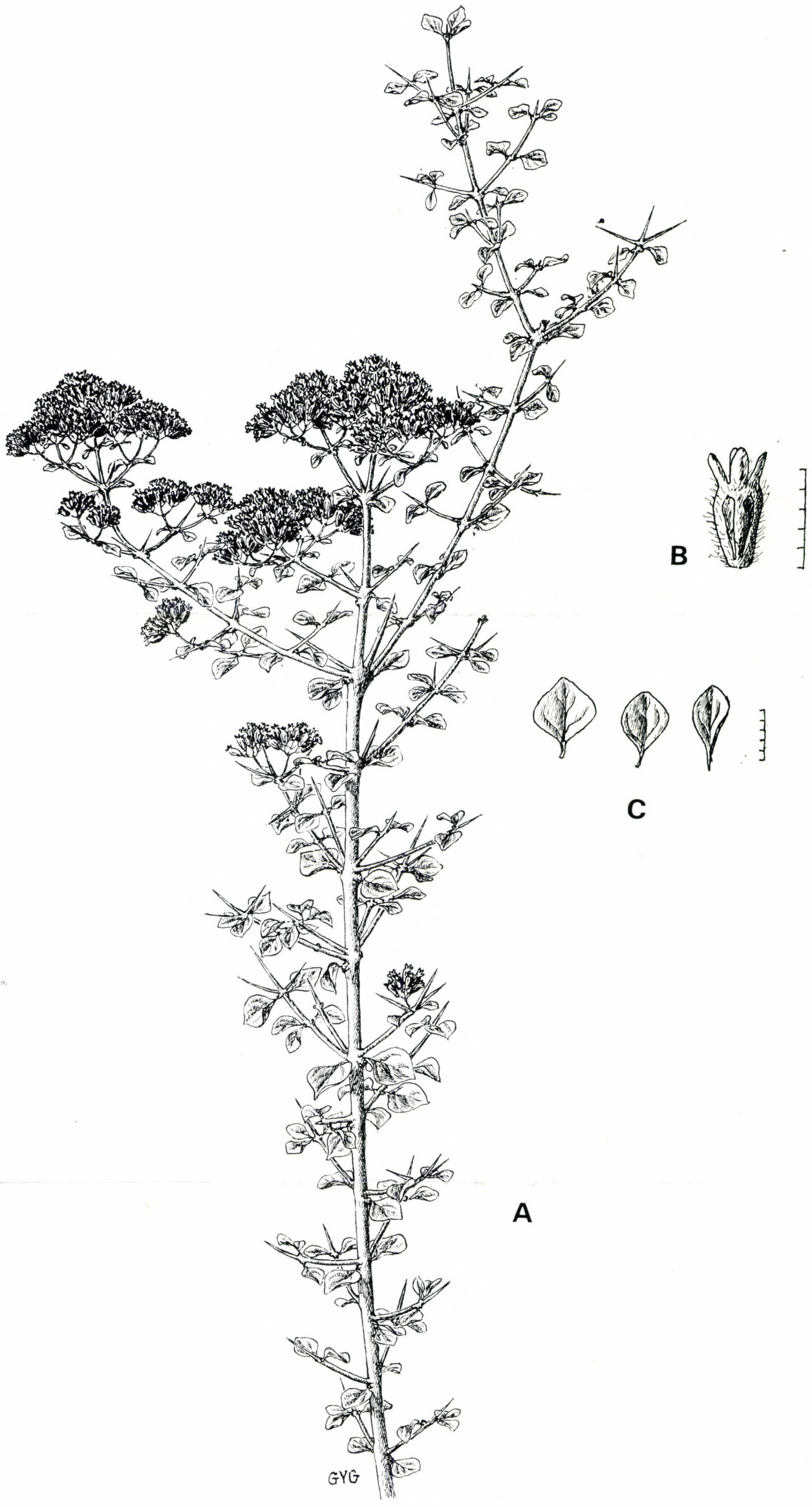

Fig. 12. Machaonia subinermis ssp. *armata* Borhidi et Fernandez; A: Aspecto general; B: Cáliz fructifero; C: Hojas. Escala: 5 mm. (Dibujo de Gisela Gyurkó)

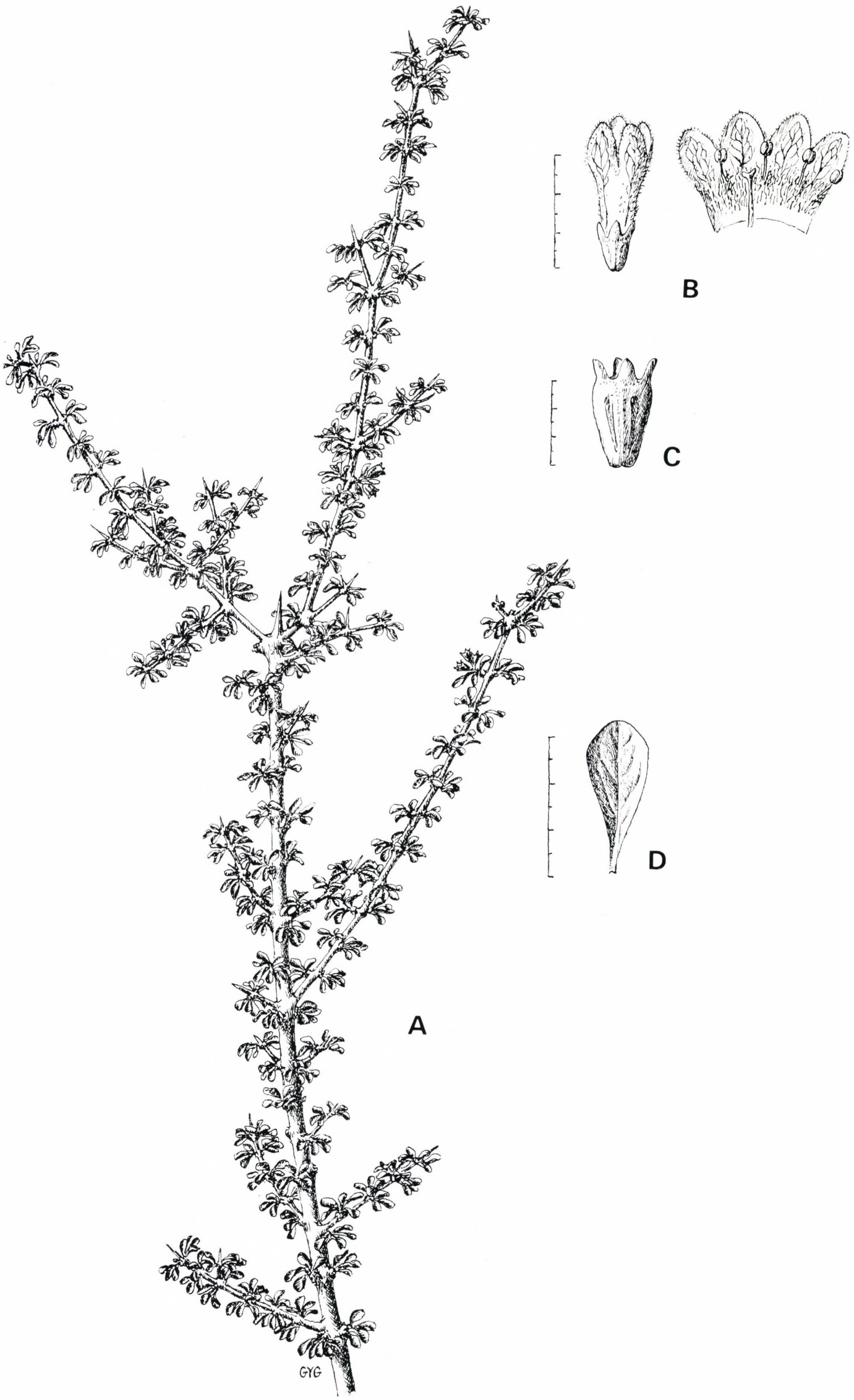

Fig. 13. Machaonia tiffina Urb.; A: Aspecto general; B: Flor y sección de la corola; C: Frutos D: Hojas. Escalas: 3 y 5 mm.
(Dibujo de Gisela GYURKÓ)

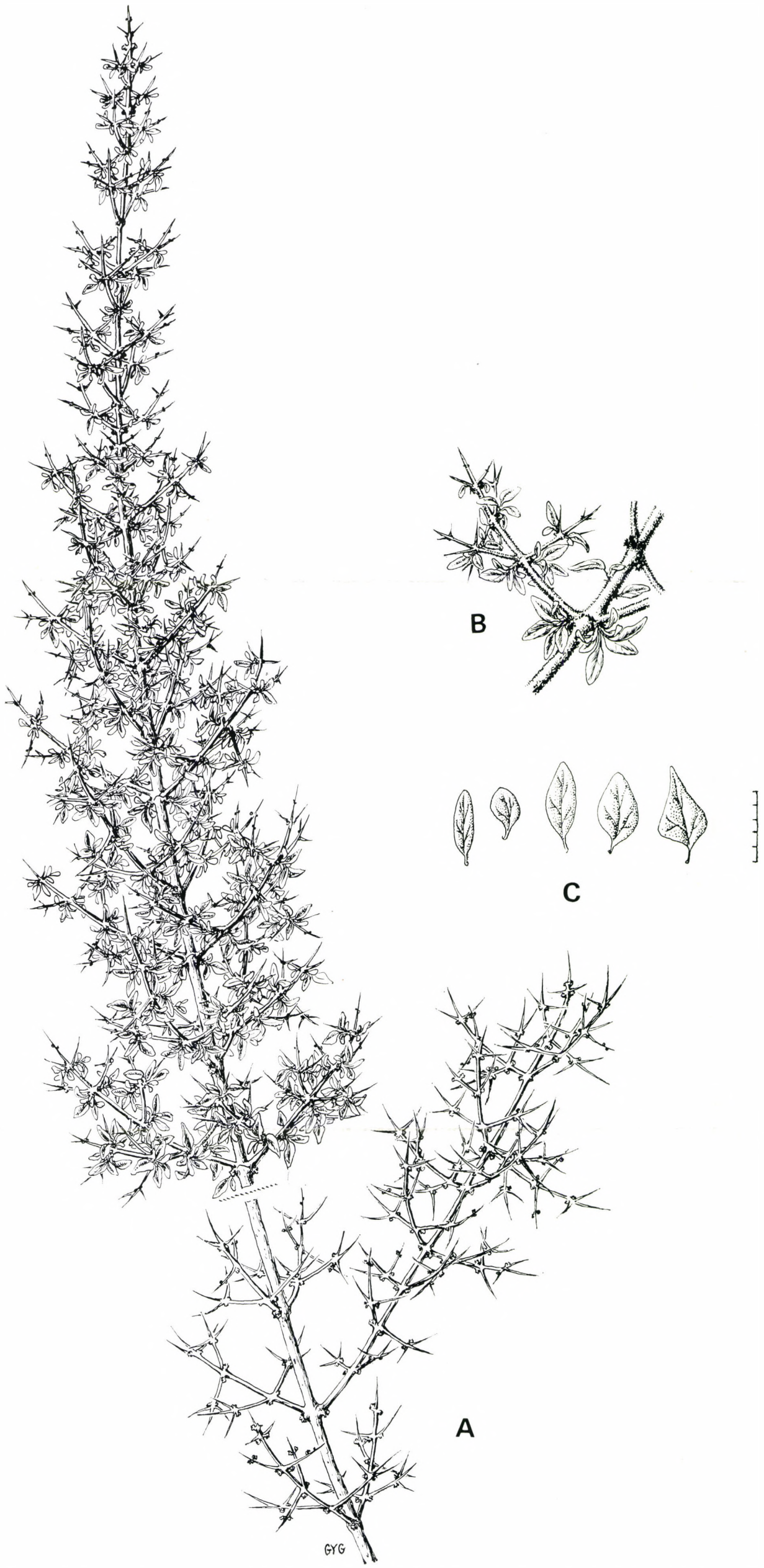

Fig. 14. Machaonia Urbaniana Standl.; A: Aspecto general; B: Parte de ramificación; C: Hojas. Escala: 5 mm. (Dibujo de Gisela Gyurkó)

oblanceoladas a lineal-obovadas de 4–7 mm de largo por 2–3 mm de ancho, redondeadas u obtusas en el ápice, largamente cuneadas en la base; nervio medio prominulo en el envés, los laterales 1–2 pares inconspicuos debajo del indumento de la hoja, el limbo densamente pubescente en ambas caras con pelos suaves diminutos blancos. Flor y fruto desconocido.

Holotipo: EKMAN 8234; Prov. Santiago de Cuba; (Oriente); dry hills at Maria Pilar, near Rio Baconao, 5. 11. 1916. F. (605073). Isotipo: S.

Esta indudablemente buena espécie del género *Machaonia* no fue recolectada desde la colecta tipica y no conocemos otro material que pertenezca a esta espécie notable, que nos permitiera completar su descripción. ALAIN H. LIOGIER (Flora de Cuba 5: 89, 1964) completó la descripción con los caracteres de la flor, basandose en un ejemplar colectado por LEÓN y SEIFRIZ en la primera mesa de Maisi en julio de 1938 (LEÓN 18110). Pero al investigar este material resultó pertenecer al género *Scolosanthus*, representando una espécie recién descrita de este género. De esta forma los organos generativos de *Machaonia urbaniana* Standl. siguen siendo desconocidos (véase: Fig. 3).

Machaonia urbinoi Borhidi et Muñiz Abstracta Bot. Inst. Tax. Oekol. Univ. Eötvös Budapest **5:** 42, 1977

Arbusto muy densamente ramificado y espinoso, de hasta 2 m de alto. Ramas adultas grisáceas, las laterales breves, terminadas en espinas gruesas sencillas o a veces ternadas. Estípulas muy cortas, aovadas, fimbriado-pelosas en el ápice. Hojas fasciculadas en los nodulos de las ramas adultas, con pecíolo de 0.4–0.8 mm de largo, obovadas, cuneadas en la base, redondeadas en el ápice, de 2–5 mm de largo y 1–3 mm de ancho, el nervio medio promínulo en el haz, poco hundido en el envés, laterales nulos en ambas caras; el limbo plano en el margen, glabro, a veces doblado, cartáceo.

Flores axilares solitarias o en cimas sentadas 3–7-floras; pedicelos de hasta 1 mm de largo, glabros o ausentes. Tubo del cáliz obtriangular, glabro, sobre el ovario abruptamente ensanchado, ligeramente turbinado. Lóbulos 5, aovados a triangulares, obtusos en el ápice, de 0.7–1 mm de largo, a veces ligeramente desiguales, glabros. Corola no vista. Fruto obcónico, cuneado en la base, ligeramente turbinado y lateralmente comprimido, de 4.5–5.5 mm de largo y de 3 mm de ancho arriba, con lóbulos persistentes cortos 5–6, glabro, 2-coco. Cocos no dehiscentes 1-spermos; la semilla oblongo-cilíndrica, endospermio carnoso.

Holotipo: Cuba; Prov. Holguin (Oriente), in fruticetis serpentinosis cacuminis montis Cerro Galano ad La Palma, prope opp. Holguin. Leg.: J. URBINO 27817 HAC, holotypus: 27818. Isotipo: en HAC, BP.

Esta espécie es semejante por su porte a *Machaonia nipensis* Borhidi et Fernandez de la cual se distingue en tener hojas glabras, inflorescencias axilares, lóbulos del cáliz 5–6, aovados, frutos grandes y lisos. Entre todas las espécies cubanas es la única que tiene cáliz y fruto 5–6-lobulados, caracter, que en todas las Antillas tiene una sola espécie mas, que es: *Machaonia martinicensis* (A. Rich.) Howard, pero esta ultima se distingue ampliamente por sus hojas grandes, rómbeas e inflorescencias apanojadas.

Machaonia urbinoi Borhidi et Muñiz es una espécie notable, que se conoce solamente de la colecta tipica (véase: Fig. 3).

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CYTOLOGICAL STUDY OF STABLE VIABLE MORPHOLOGICAL CHANGES APPEARING IN *AMARANTHUS* WEED POPULATIONS OF MAIZE MONOCULTURES*

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Morphological changes in the inflorescence of *Amaranthus* populations in 15 years old maize monoculture and the cytology of these changes, were studied.

Morphological mutants of inflorescence in the *A. retroflexus* strain were of the following types: "nose-shaped", "blant", "forked", "double-forked", in the *A. chlorostachys* strains: "beaked", "glomerate".

The chromosome number of somatic cells in *A. retroflexus* is 2n = 34. In the "nose-shaped" mutant it was 2n = 34; in the "forked" 2n = 34; in the "blant" 2n = 34; while in the "double-forked" 2n = 68. The mutants of *A. chlorostachys* had the following chromosome numbers: "beaked" 2n = 34; "glomerate" 2n = 34. Thus, the "double-forked" mutant of *A. retroflexus* proved to be tetraploide. This is reflected in the morphology of its spike, too.

Since the tetraploide mutant has sofar never been found in soils not treated with herbicides, it is considered probable by the authors that its appearance is consequence of herbicide treatment.

Introduction

In the course of research into maize-ecosystems carried out at the Plant Protection Institute the morphology of the inflorescence of *Amaranthus* strains occurring in 15 years old maize monoculture in Agárd-Tükröspuszta (County Fejér) was studied. A number of morphological changes were observed in the populations of *A. retroflexus* and *A. chlorostachys*.

Morphological mutants do not seem to form the subject of genetical studies at present. The authors, however, find it noteworthy to publish their observations, since it is a proven fact that pesticides cause genetical changes (EPSTEIN and LEGATOR 1974; GRANT 1978).

In the present study it was aimed at to find out whether morphological changes in the inflorescence (hereafter: spike) are acccmpanied by changes in cytology.

Material and methods

The test material was collected during 1979 and 1980 in County Fejér, in the maize monoculture at Agárd-Tükröspuszta where a herbicide ("Hungazin PK") containing atrazine had been used for 15 years.

The samples represented *A. retroflexus* and *A. chlorostachys* mutants with spikes deviating from normal. The stability of the mutants was proven by propagation from seed during 1981. Of the plants grown from seed only those were studied which maintained their morphological character. For the sake of comparison samples were taken also from *A. retroflexus* and *A. chlorostachys* with normal spike.

* Maize-ecosystem investigations No. 29.

Cytological tests were carried out on the meristematic cells of the root top in six seedlings the spikes of which deviated from the normal and in seedlings of normal character. Of the six mutants investigated four belonged to strain *A. retroflexus* and two to *A. chlorostachys*. Roots of 3–5 mm length of the seedlings were treated in a 0.002 M 8-oxykinoline solution for 1–2 h at about 14 °C.

Fixing and staining were carried out by methods as described earlier (PUSZTAI—GILYAROVSKAYA 1973) and dispersed preparations were made.

Results and discussion

The fasciation of the spike is a frequent symptome of morphological abnormality with *Amaranthus* strains (PRISZTER 1950).

A great number of publications appeared on the genetical effect of triazines in plants of higher order. The significant genetic activity of simazine and atrazine in barley was shown in serial tests, including changes in morphology (WUU and GRANT 1966, GRANT 1972, TOMKINS and GRANT 1972). GRICAENKO and MISHKUROVA (1976) found that the dose of simazine as applied in cultivation and its multiples have frequently caused aberrations in the chromosomes of maize, which increased progressively with the dose. However, according to other authors the above mentioned chemicals had no genetical effect on maize (LOGVINENKO et al. 1981) or on barley (BELOVA et al. 1981). Related publications prove that investigations into the mutagenic activity of simazine and atrazine had contradictory results.

BEHERA and PATNAIK (1977) applied chemical (diethylsulphate) mutagenes and succeeded in producing viable morphological mutants in the *A. hypochondriacus* populations. At the same time they found that the wide scale of changes in morphology observed in M_1 did not pass over into M_2. Thus, these may be considered modifications. Chromosomal aberrations were not found in the pigmy-mutants they detected, these mutants, therefore, are probably gene mutants. In the mutants collected of both *A. retroflexus* and *A. chlorostachys* the fasciation of the terminal spike was observed as in the mutants artificially induced (BEHERA and PATNAIK 1977). In this study six mutants were separated. In the *A. retroflexus* strain "nose-shaped", "blant", "forked" and "double-forked"; in *A. chlorostachys* "beaked", "glomerate" (Fig. 1).

As it can be seen in Fig. 2 the chromosomes are of approximately equal length and generally small, therefore they are not suitable for more detailed cytological investigation (morphology, aberrations and stripe-treatment). The small size of chromosomes, on the other hand facilitates the establishment of their number. The chromosome number of *A. retroflexus* was found to be $2n = 34$; in the morphological mutants: $2n = 34$ for the "nose-shaped", $2n = 34$ for the "blant", $2n = 34$ for the "forked", while $2n = 68$ for the "double-forked". The chromosome number in *A. chlorostachys* was $2n = 34$, in the "beaked" mutant $2n = 34$ and in the "glomerate" mutant $2n = 34$.

Fig. 1. Normal and spike-morphological mutants of strains *A. retroflexus* and *A. chlorostachys*. 1–5: *A. retroflexus*; 6–8: *A. chlorostachys*. 1. Normal, 2. "nose-shaped", 3. "blant", 4. "forked", 5. "double-forked", 6. normal, 7. "beaked", 8. "glomerate"

Thus the "double-forked" mutant of *A. retroflexus* was shown to be tetraploide.* This is reflected in its morphology, too (Table 1). It is not proven

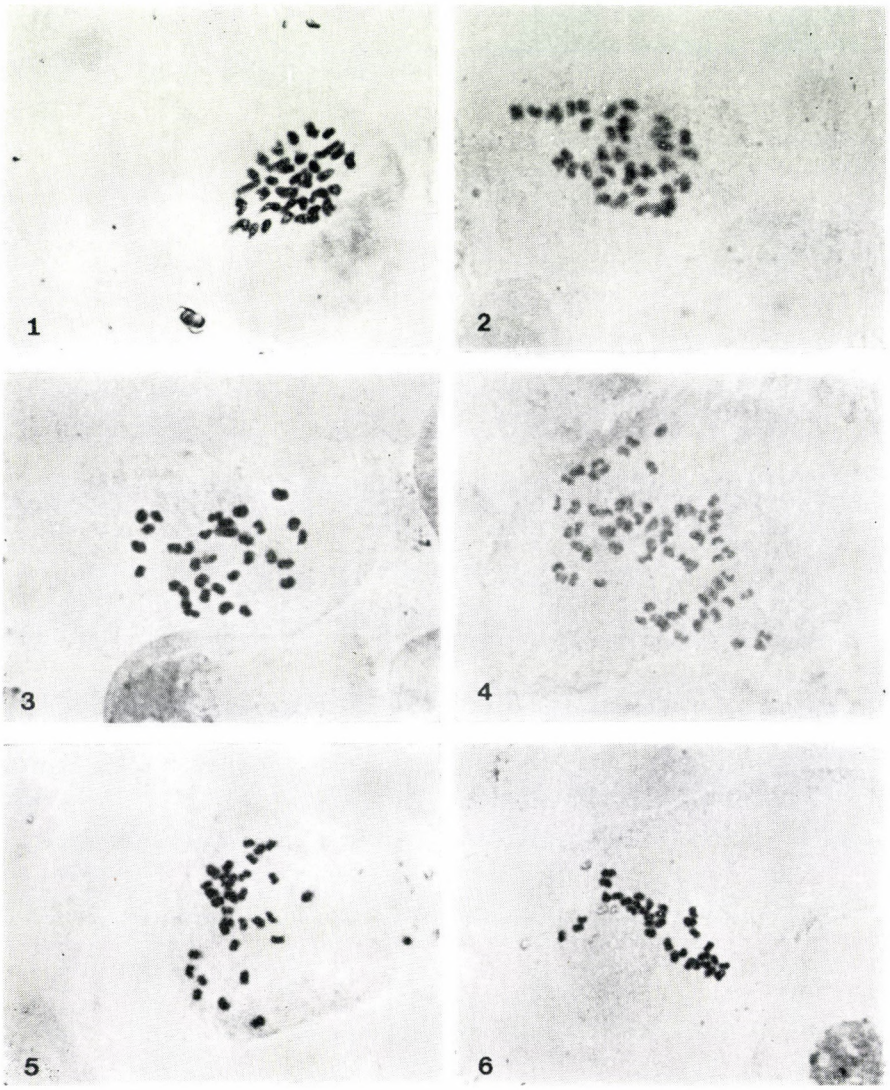
* Description of the morphology of the tetraploide mutant of *A. retroflexus*:

Plant height: 110–130 cm. Stem erect, thick (1 cm), not branched. The whole plant is of yellowish-green colour, the stem is densly flocculent. The leaves have long stalk and are of rhomboidal-oval shape, gradually tapering to the point. The flowers are very dense in the spike. The spike in full is of 15 cm length. The flowers sit in the armpit of prickly-rigid prophylls of 5–7 cm length. The five leaves of the perygon are 3–4 cm long, narrow, of blade shape. The fruit is dehiscent capsule. The seeds are lentil-shaped with sharp edge, of 1.3 mm diameter, bright black.

Table 1

Comparison between the important measurements of the

	Height of plant, cm	Length of leaf, cm			Width of leaf, cm		
		1st level	2nd level	3rd level	1st level	2nd level	3rd level
Diploide	95	4	6	7	2	3.5	4.4
Tetraploide	120	5	7.5	9	3	5	5.5



diploide and tetraploide specimen of A. retroflexus

Terminal-spike, cm		Length of 2nd prophyll, mm	Length of leaf of perygon, mm	Seed	
Length	Width			Shape	Diameter, mm
10	2.5	5	2.5	lentil	1
15	4	7	4	lentil	1.5

directly that the new polyploide mutant is the consequence of continuous application of herbicide and it may be conceived its occurrence under conditions free of chemicals (GRANT 1959). The probability, however, of the new polyploide mutant being the result of the mutagenic effect of herbicide treatment cannot be excluded, since it was not encountered yet in fields not treated with chemicals.

Acknowledgements

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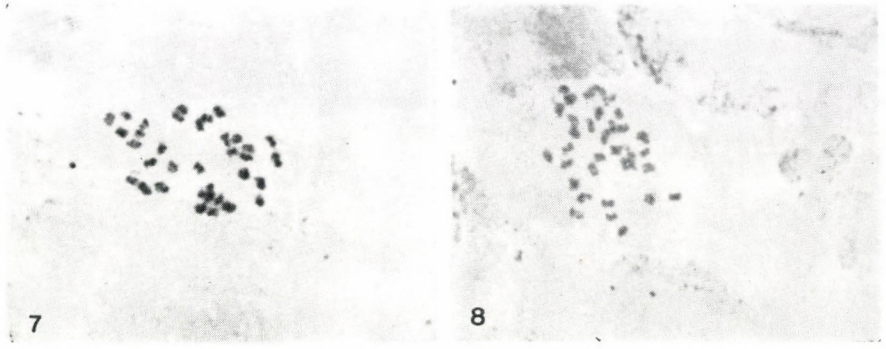

Fig. 2. Chromosome number of somatic cells in *A. retroflexus* and *A. chlorostachys* strains and in their morphological mutants (×1500). 1–4: *A. retroflexus*; 5–6: *A. chlorostachys*; 7–8: basic chromosome number in *A. retroflexus* and *A. chlorostachys*. 1. "Nose-shaped", 2. "blant", 3. "forked", 4. "double-forked", 5. "beaked", 6. "glomerate", 7. *A. retroflexus*, 8. *A. chlorostachys*

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CYTOLOGICAL INVESTIGATION OF *SCILLA BIFOLIA* POPULATIONS IN HUNGARY. I.

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In the framework of the complex taxonomical research programme of the Botanical Research Institute of the Hungarian Academy of Sciences a cytotaxonomical investigation of the *Scilla bifolia* group has been started by the authors on living population samples transplanted to experimental parcels in the Institute. As a result the chromosome number of 31 populations has been determined out of which there are 19 diploid ($2n = 18$), 11 tetraploid ($4n = 36$) and 1 hexaploid ($6n = 54$) populations. Considering their localities the identification of polyploids may be regarded as a new finding for Hungary, especially what concerns the hexaploid population, which has not been described yet for Transdanubia in the literature. A new result is that in the close proximity of diploid populations vegetating in the upper Danube area in Hungary a polyploid group has been also found with its morphological characters very similar to the diploids. The diploids of the mountainous area of Northern Hungary that have been examined up to now are mostly tetraploids, but in the Zemplén Mountains well separated diploid populations have been found. The investigations outlined in the paper partly support, partly extend the findings of SPETA (1977a, b) obtained for the territory of Hungary by presenting new results for the species of the group described by him. It is concluded that *Scilla vindobonensis* may be regarded as a characteristic element of Pannonian flora, what is supported by a detailed examination of the karyotype of diploid populations made by the authors.

Introduction

The comparative cytotaxonomic analysis of *Scilla bifolia* populations occurring in the territory of Hungary is conducted in the framework of a complex taxonomic research programme carried out at the Botanical Research Institute of the HAS. The investigation is aimed at contributing to the more detailed knowledge of the taxonomic value of these populations. As a first step the chromosome number of populations transplanted to experimental parcels within the area of the institute has been established, and the karyotype analysis of individual chromosome sets has been performed. As pointed out by STEBBINS (1959), the fundamental process in evolutionary cytology is the determination of the number of chromosomes.

If the starting point for systematization is the principle of evolution, then significance of chromosomes will differ strongly from that of other, morphological, ecological or physiological characters. Namely, the differences in chromosomes reveal more directly the genetical content and degree of organization of an individual organism. The variances in their staining (i.e. the ratio of euchromatin to heterochromatin) show the regularity and timedness of gene functioning in most cases. With a change in caryotype the linkage and rate of recombination of genes is also modified. This is why following LEVITZKY (1931) the concept of "caryotype evolution" was introduced by STEBBINS (1950, 1958). On the chromosome set of each species

a certain degree of asymmetry can be noticed which can be used for the classification of the caryotypes. It was found that evolution leads to an increased asymmetry, as demonstrated by examinations of *Crepis*, *Haplopappus* and *Aster* species (STEBBINS 1971). A similar tendency was observed by KAPOOR and LÖVE (1970) at Ranunculus species. An increased symmetry coupled with a decreased chromosome number, observed by STEBBINS (1971) for Lycoris species, is a very rarely occurring phenomenon for plants.

Caryotype variations are frequently connected to the formation of an "adaptive gene cluster" ("adaptive gene cluster hypothesis", STEBBINS 1971). Its origin can be traced back mostly to two types of chromosomal variations, i.e. to inversion and translocation. In the case of plants, inversion heterozygocy can be deduced only from meiotic "bridge and fragment" associations (in the case of paracentric inversions). Therefore such variations in plants are observable rather at the species level only. As a consequence of inversion the strength of linkage of genes within the chromosomes is significantly modified and their new adaptive arrangement may appear. At the same time, as a crossing-over suppressor, inversion may lead to the separation of populations. Through translocation a rearrangement between linkage groups may take place. For their detection the meiotic associations of the heterozygote state are also used. Thus both inversion and translocation may result in a caryotype change.

SPETA's investigations pointed out the fact that the *Scilla bifolia* L. taxon, which has been considered to be uniform up to now, and is spread in Europe and Asia Minor excluding the Iberian Peninsula and parts of Europe covered by ice during glacial periods, actually represents an agglomeratum including a number of species well separated from each other. On the basis of the examination of specimens collected in Austria and at other localities in the area, in 1976 SPETA divided the genus (incorporating the genus *Chionodoxa* Boiss.) into the following four sections: *bifolia*, *vindobonensis*, *nivalis* and *luciliae* (= *chionodoxa*). From the first section *Scilla bifolia* L. ssp. *bifolia*, *Scilla bifolia* L. ssp. *danubialis* Speta and *Scilla drunensis* Speta and from the second section *Scilla vindobonensis* Speta can be found in Austria, which taxons extend also to the area of neighbouring countries. In addition to morphological differences, the necessity to separate these taxons has been justified also by comparative caryotype investigations by SPETA and his colleagues, among them mainly by J. GREILHUBER. Their results settled definitely that in consequence of its tetraploidy the taxon which has been described until recently under the name *S. bifolia* L. ssp. *drunensis* is in fact an independent species, the *S. drunensis* Speta (SPETA 1976), as opposed to the very similar *S. bifolia* ssp. *danubialis* taxon, which, similarly to the prototype, is a diploid. By preparing the caryotypes of the new taxons it turned out that in this respect the two subspecies of *S. bifolia* and the *S. drunensis* are very similar to each other, in spite of the fact that the latter is a tetraploid (Fig. 4). The caryotype of *S. vindobonensis*, however, differs so strongly from that of the others, that this difference in itself justifies the classification of this taxon to a separate section (GREILHUBER and SPETA 1979). Later a diagramme outlining the relationships between the species in the *S. bifolia* group and compiled on the basis of DNS and heterochromatin content has been also published (GREILHUBER 1979). SPETA's results demonstrated convincingly the great variability of *Scilla* genus even over a relatively small part of the area. This fact, among others, drew our attention to the high probability of a similar behaviour of *Scilla* populations in Hungary and consequently to the surprises that can be expected from their detailed cytotaxonomic study. Such a study may result also in the veryfication, extension or, eventually, modification of SPETA's conclusions or hypotheses regarding Scilla species occurring in Hungary, and thus it may help us to a more complete knowledge of *Scilla* genus.

Material and methods

I. Experimental plant material

Our experimental material consists of living specimens collected from various localities in Hungary between 1979 and 1981. The specimens are cultivated on a uniform soil on the same site in the Institute. Altogether the chromosome set of 31 population samples has been analysed, the data of which are described below in the following order: serial number of sample, name of nearest settlement, country, geographical area — closer description or name of the locality, association, approximate altitude above sea level, date of collection, grid number on the flora map of Central Europe. In the following list the localities are grouped into five large areas of the country, which indicate not only geographical differences but in many cases a taxonomic separation as well.

Upper and Central Danube Valley

1. Mosonmagyaróvár, Győr co., after the 155 km mark along the main road No. 1., *Querco-Ulmetum populetosum*, 80 m, 5 May, 1981, 8169; **2.** Zsejkepuszta, Győr co., Szigetköz, bank of the Danube along the roadway, *Salicetum albae-fragilis*, 80 m, 8 May, 1981, 8271; **3.** Vámosszabadi, Győr co., Szigetköz, before the frontier bridge, *Querco robori-Carpinetum*, 80 m, 8 May, 1979, 8272; **4.** Győr, Győr co., Püspökerdő, right after Pinyédi bridge, *Fraxino pannonicae-Ulmetum*, 100 m, 8 May, 1979, 8371; **5.** Kisoroszi, Pest co. Isle of Szentendre, *Fraxino pannonicae-Ulmetum populetosum*, 80 m, 4 May, 1979, 8180; **6.** Budapest, Népsziget, garden of the Water Board, *Querco-Ulmetum populetosum*, 80 m, 28 March, 1981, 8480; **7.** See no. 6., white flowered; **8.** Ráckeve, Pest co., Angyali isle, *Salicetum albae-fragilis*, in the place of a former *Querco-Ulmetum* association, 80 m, 30 April, 1979, 8879.

Western and Central Transdanubia

9. Alsóújlak, Vas co., on the right side of the roadway after the settlement, *Querco robori-Carpinetum*, 160 m, 14 May, 1981, 8966; **10.** Ikervár, Vas co., forest and meadow of Ikervár, *Querco robori-Carpinetum*, 150 m, 12 April, 1979, 8767; **11.** Doba, Veszprém co., Bakony Mts., south-eastern slope of Mt. Somlóhegy, *Querceto petraeae-Carpinetum*, 350 m, 26 May, 1980, 8870; **12.** Pápakovácsi, Veszprém co., Gannai forest, *Aegopodio-Alnetum quercetosum* cult., 200 m, 12 April, 1979, 8771; **13.** Bakonypölöske, Veszprém co., Kupi forest, bank of Kőrös stream, *Aegopodio-Alnetum quercetosum*, 200 m, 12 April, 1979, 8770; **14.** Nadap, Fejér co., Velencei Mts., north of the settlement, along the roadway, *Aceri tatarico-Quercetum ornetosum*, 250 m, 10 April, 1981, 8777.

Eastern and Southern Transdanubia

15. Simontornya, Tolna co., Pálfai forest, behind the sheepfold of the co-operative farm, *Querco robori-Carpinetum*, 200 m, 30 March, 1981, 9277; **16.** See no. 15., a type of small stature; **17.** Pécs, Baranya co., Mecsek Mts., Tubes ridge, *Tilio argenteae-Fraxinetum*, 500 m, 11 April, 1981, 9875; **18.** Pécs, Baranya co., Égervölgy, *Helleboro odoro-Fagetum*, 200 m, 10 April, 1981, 9875; **19.** See no. 18., a little, slender type; **20.** Nagyharsány, Baranya co., Villányi Mts., Szársomlyó, Ördögvölgy, *Asperulo taurinae-Carpinetum*, 200 m, 10 April, 1981, 0176; **21.** Nagyharsány, Baranya co., Villányi Mts., Szársomlyó, above the Szoborpark, *Tilio argenteae-Fraxinetum*, 300 m, 10 April, 1981, 0176; **22.** Kisjakabfalva, Baranya co., bank of the Karasica stream, *Fraxino pannonicae-Ulmetum praeillyricum*, 150 m, 10 April, 1981, 0176.

Northern Central Range

23. Nagybörzsöny, Pest co., Börzsöny Mts., Summit of Mt. Nagyhideghegy, *Tilio-Fraxinetum* and *Aconito-Fagetum*, 850 m, 27 April, 1979, 8079; **24.** Cserépfalu, Borsod co., Bükk Mts., valley of Hór stream, *Melico-Fagetum*, 250 m, 17 April, 1979, 8089; **25.** Répáshuta, Borsod co., Bükk Mts., northern slope of Mt. Kerekhegy, *Aconito-Fagetum*, 500 m, 17 April, 1800, 7989; **26.** Felsőtárkány, Heves co., Bükk Mts., ridge of Mt. Várhegy, *Corno-Quercetum*, 600 m, 29 April, 1981, 8088; **27.** Répáshuta, Borsod co., Répáskúti valley, *Melico-Fagetum*, 450 m, 30 April, 1981, 7939; **28.** Makkoshotyka, Borsod co., Zemplén Mts., valley of Völgypatak stream, *Querco robori-Carpinetum*, 200 m, 8 May, 1980, 7695; **29.** Füzérradvány, Borsod co., Zemplén Mts., castle park of Vilypuszta, *Quercetum roboris* cult., 150 m, 8 May, 1980, 7595.

Territory east of the river Tisza

30. Új szentmargita, Hajdú co., Margitai forest, *Galatello-Quercetum*, 100 m, 22 May, 1980, 8292; **31.** Doboz, Békés co., Szanazugi forest, *Querco-Ulmetum*, 100 m, 29 April, 1979, 9293.

Table 1

Number of chromosomes for investigated populations of Scilla bifolia

No. of sample	Locality	No. of chromosomes
Diploid populations		2n = 18
1	Mosonmagyaróvár	
2	Zsejkepuszta	
4	Győr	
5	Kisoroszi	
6	Budapest, Népsziget	
7	Budapest, Népsziget (little)	
8	Ráckeve	
11	Doba	
12	Pápakovácsi	
13	Bakonypölöske	
17	Pécs, Tubes	
18	Pécs, Égervölgy	
19	Pécs, Égervölgy (little)	
20	Nagyharsány, Ördögvölgy	
21	Nagyharsány, Szársomlyó	
22	Kisjakabfalva	
28	Makkoshotyka	
29	Füzérradvány	
31	Doboz	
Tetraploid populations		4n = 36
3	Vámosszabadi	
9	Alsóújlak	
10	Ikervár	
15	Simontornya	
16	Simontornya (little)	
23	Nagybörzsöny	
24	Cserépfalu	
25	Répáshuta, Kerekhegy	
26	Felsőtárkány	
27	Répáshuta, Répáskúti-völgy	
31	Újszentmargita	
Hexaploid population		6n = 54
14	Nadap	

II. Method of cytological analysis

The root samples were taken at a sprout length of 3–4 cm in the second half of February from bulbs raised in pots held in a cold-house. After a four-hour colchicine (0.05%) treatment and a subsequent fixing in Farmer-fixer (alcohol and acetic acid mixed at a ratio of 3 : 1), the samples were washed in alcohol of 70% and stained by the well known technique using aceto-carmine. The photomicrographs were taken by a photomicrographic apparatus of the type MF Zeiss attached to a microscope NFpk 2, using ORWO NP 15 film, with an objective of ×100 and an ocular of ×P4. The karyotypes were prepared by evaluating 5 cells for each population. Because of the large size of the chromosomes it was the methaphase which turned out to be the most suitable for the analysis, with a weaker overlapping of the maximally contracted chromosomes as in the previous phase. In order to prepare the karyotype the arm-ratio (AR), relative length (RL) and centromeric index (CI) of chromosomes were measured at a magnification of 1500. Because the prepared diploid karyotypes are very similar to each other, the results for only two populations are presented in detail, for the rest a number of photographic plates are shown.

Results

The number of chromosomes for the populations under investigation are summarized in Table 1. Accordingly, most of them, i.e. specimens from 19 localities have a diploid (2n = 18) chromosome number; 11 populations are tetraploid (4n = 36) and 1 population is hexaploid (6n = 54). A number of diploid metaphase cells from different localities are shown in Plate I. The chromosome sets of diploid populations are very similar to each other both morphologically and regarding their size. The detailed karyotype analysis of diploid sample populations Nos 2 and 31 is shown in (Plate II.). The diploid chromosome set is composed of metacentric and sub-metacentric chromosomes. The largest chromosome pair has a satellite. This pair of chromosomes is present in a stable manner in almost all of the diploid cells (marked by arrows in Plate I). Chromosome sizes for sample 2 are included in Table 2, while the averages

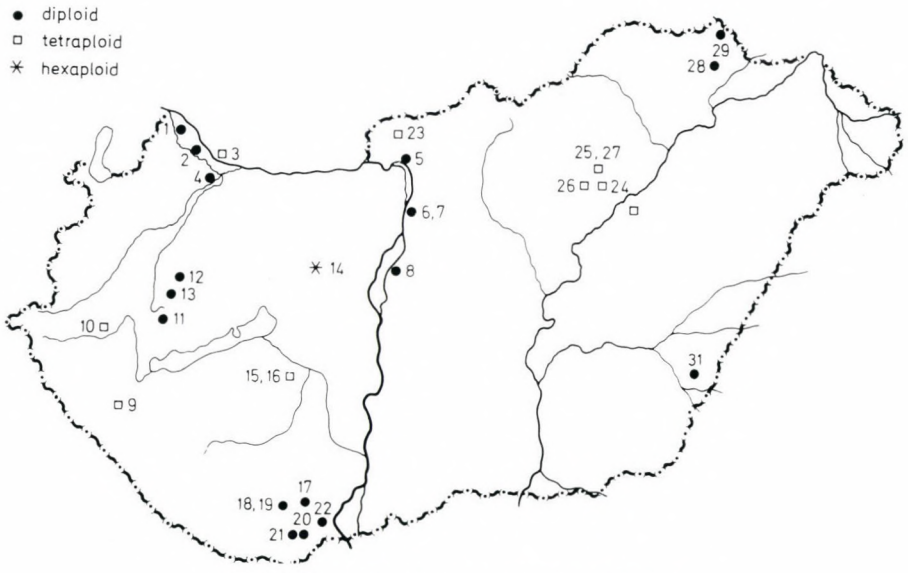

Fig. 1. Localities of the examined populations

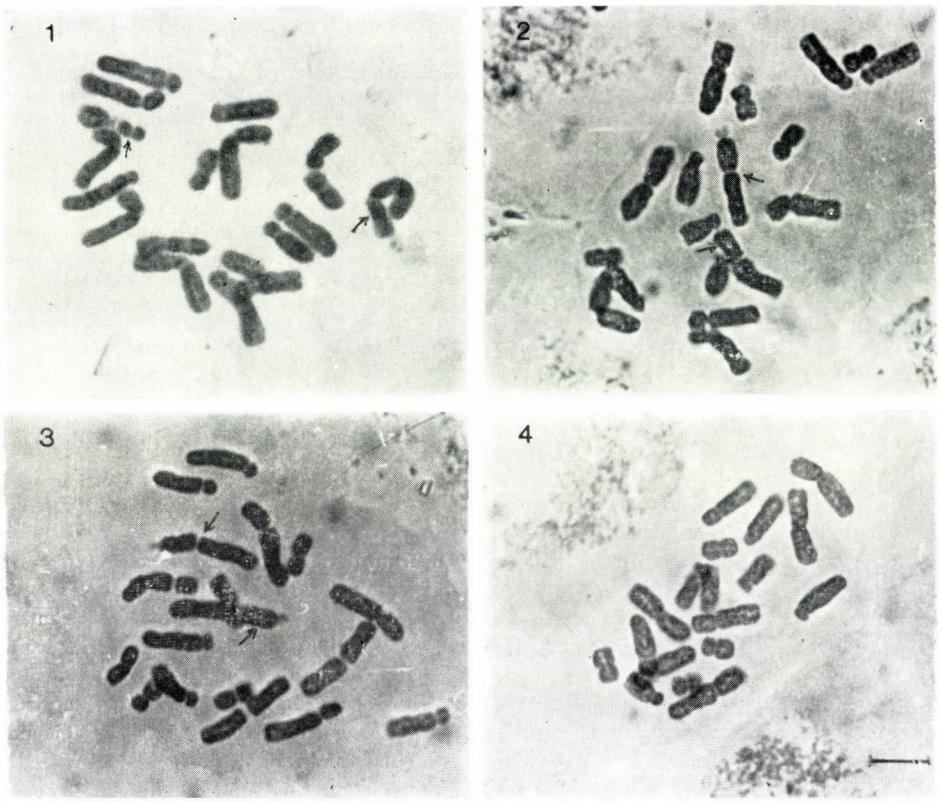

Plate I

Diploid metaphase cells of *Scilla bifolia* (2n = 18). SAT-chromosomes marked by arrows. Bar: 10 nm. 1. Locality 1, Mosonmagyaróvár; — 2. Locality 4, Győr; — 3. Locality 8, Ráckeve; — 4. Locality 18, Pécs

Table 2

Data of chromosomes of population sample 2

Chromosome pair No.	AR	RL	CI
1	1.145	1.02	0.525
2	1.20	1.045	0.525
3	2.00	1.04	0.64
4	1.875	1.00	0.65
5	2.565	1.025	0.70
6	3.665	1.07	0.745
7	4.165	0.975	0.82
8	3.815	1.00	0.79
9	1.10	1.045	0.50

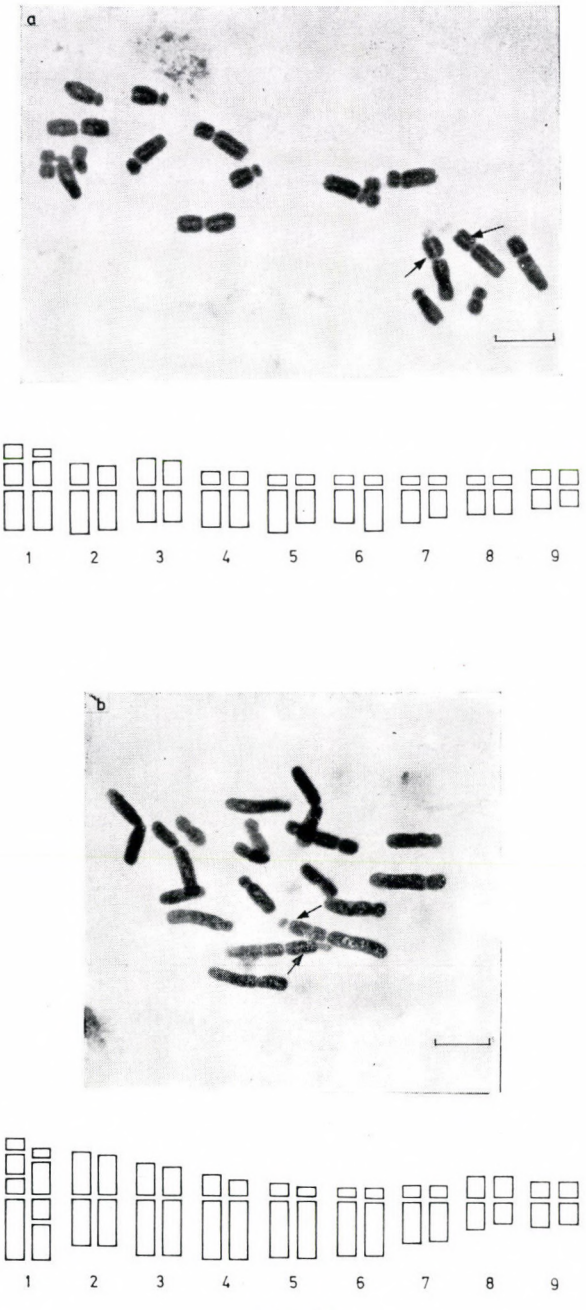

Plate II

Karyotype and karyograms of diploid *S. bifolia* populations. SAT-chromosomes marked by arrows. Bar: 10 nm. (a) Locality 2, Zsejkepuszta, (b) Locality 31, Doboz

Table 3

Average data for meta- and sub-metacentric chromosomes of sample 2

	$\bar{x}$	s
Metacentric		
AR	0.58	1.31
CI	0.26	0.60
Sub-metacentric		
AR	1.08	3.59
CI	0.36	1.221

Table 4

Data of chromosomes of population sample 31

Chromosome pair No.	AR	RL	CI
1	1.065	1.00	0.515
2	1.45	1.025	0.59
3	1.235	0.965	0.53
4	1.815	0.96	0.62
5	1.745	0.985	0.63
6	2.69	1.00	0.725
7	6.71	1.04	0.90
8	4.74	1.00	0.825
9	3.5	0.975	0.76

Table 5

Average data for meta- and sub-metacentric chromosomes of sample 31

	$\bar{x}$	s
Metacentric		
AR	0.523	1.17
CI	0.25	0.565
Sub-metacentric		
AR	1.61	5.36
CI	0.377	1.249

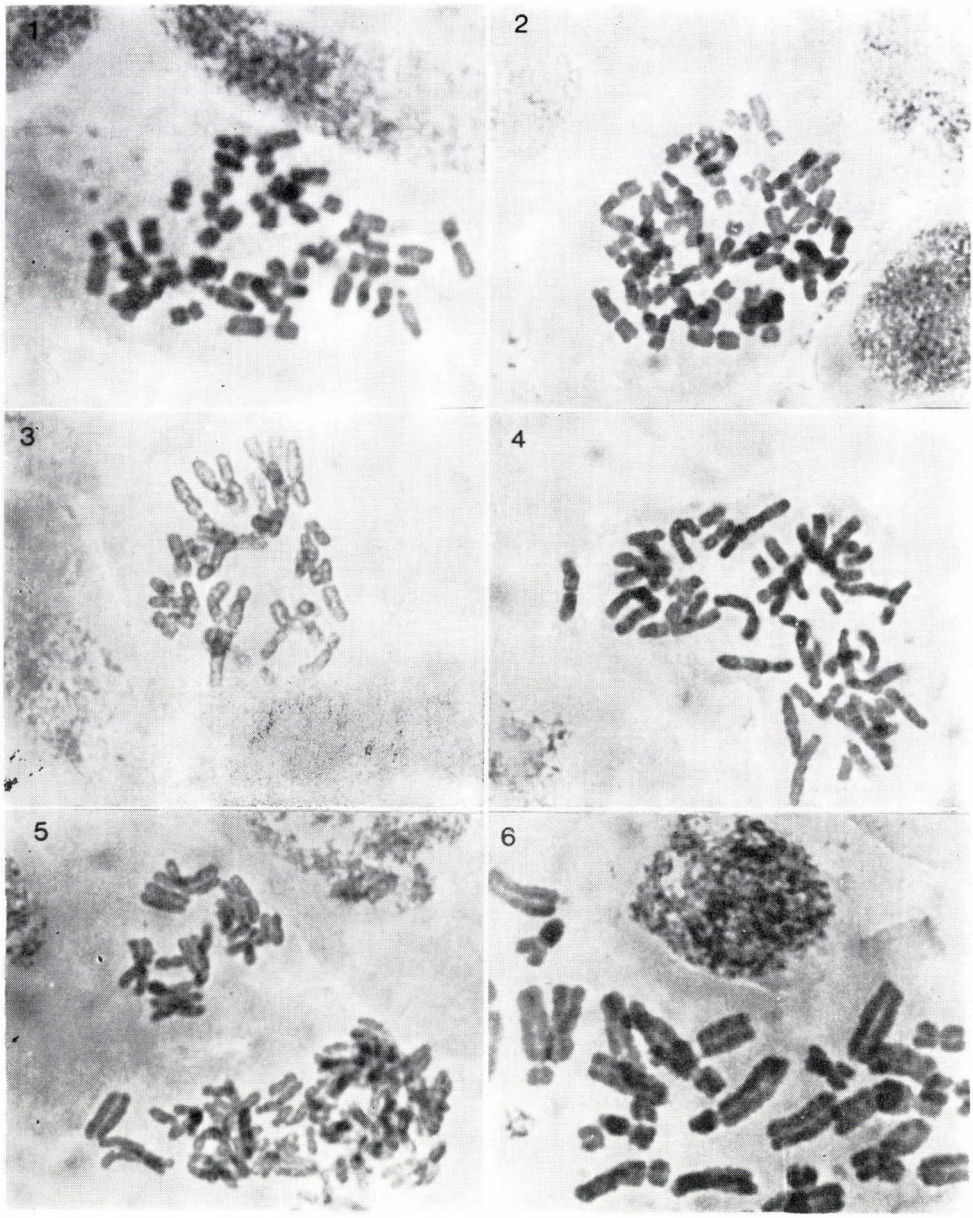

Plate III

Polyploid metaphase cells of *Scilla bifolia* populations. Bar: 10 nm. — Localities: 1, 3, Vámosszabadi, tetraploid, 2n = 36; — 2. 9, Alsóújlak, tetraploid, 2n = 36; — 3: 26, Felsőtárkány tetraploid, 2n = 36; — 4. 23, Nagybörzsöny, tetraploid, 2n = 36; — 5. 14, Nadap, hexaploid, 6n = 54; — 6. 15, Simontornya, tetraploid cell with chromosomes of great size

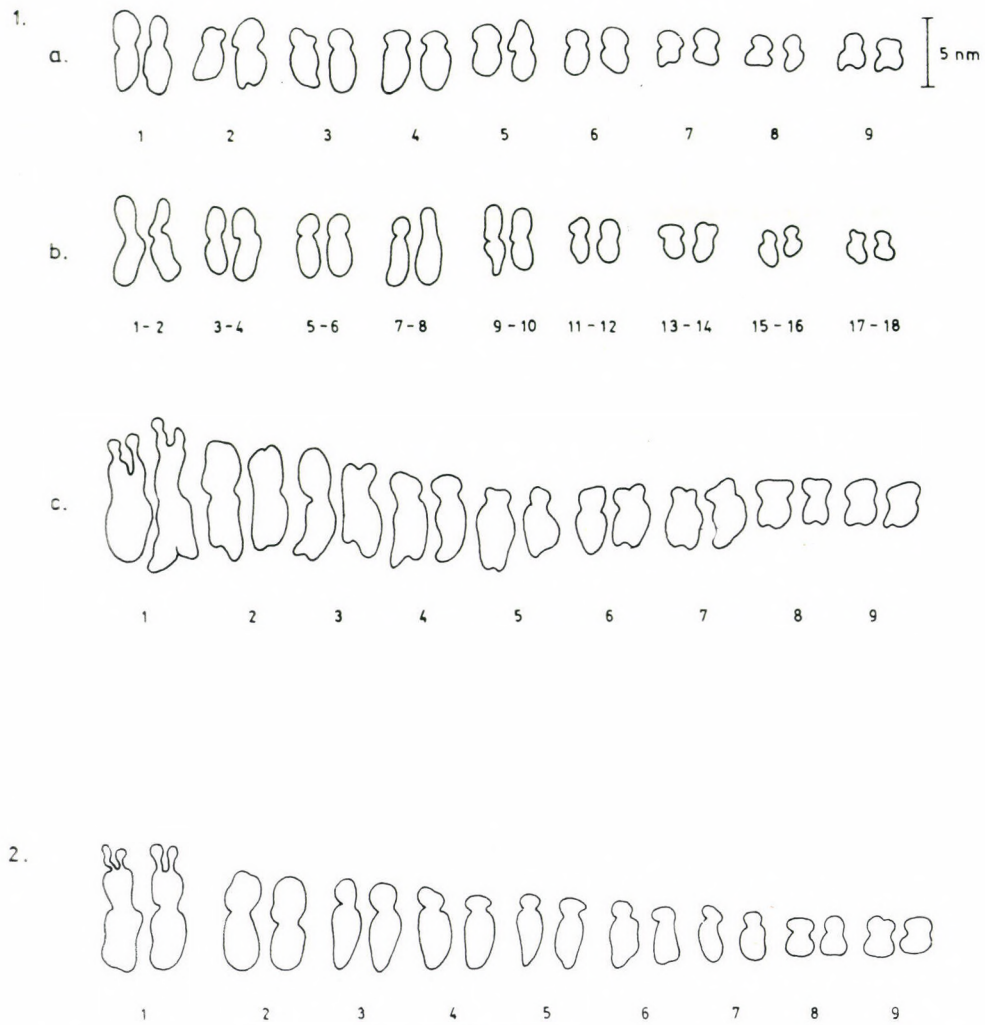

Plate IV

Karyotype comparison between the population in loc. 2 and SPETA's species. 1. Karyograms of SPETA's species (Plant. Syst. Ev. 127/1977). (a) *S. bifolia* L. ssp. *danubialis* Speta; (b) *S. bifolia* L. ssp. *drunensis* Speta; (c) *S. vindobonensis* Speta. 2. Karyogram of the diploid taxon in locality 2, Zsejkepuszta

($\bar{x}$) and standard deviations (s) for the chromosome pairs are shown in Table 3. Tables 4 and 5 contain similar data for sample 31. A comparison of the data for the two samples shows that the AR and CI-values for metacentric chromosomes are in close agreement in the two samples, the CI values for sub-metacentric chromosomes are also nearly identical, but for them a difference appears already in the AR values; namely, the average AR value of sample 31 exceeds that of sample 2 by nearly 30%.

In the karyograms of *S. bifolia* taxa investigated by SPETA (1977) there are 4 and 6 sub-metacentric chromosomes for the first two and for the third taxon, respectively (Plate IV).

Moreover, the first chromosome pair in the cells of the third taxon has a clearly visible satellite, while the latter is absent in the first two taxa. Exactly these differences, in addition to the differences in chromatine content, led to the setting up of the *Luteoscilla* section. Comparing our results to SPETA's investigations it appeared that among the diploid populations which had been analysed in detail only the karyograms of those vegetating in the Danube Valley and in eastern Hungary possess such a SAT-chromosome pair (Plate I). This karyotype exhibits a great similarity to the karyotype of *S. vindobonensis* shown in Plate IV regarding its other characteristics, too.

Among the polyploid samples there are 11 tetraploid and 1 hexaploid ones. The latter one is especially interesting because it represents an entirely new result for Transdanubia. This degree of ploidy is mentioned by SPETA for populations in the Bükk Mountains, but it has not been confirmed by our investigations. Looking at the chromosome set of the polyploid populations shown in Plate III it appears immediately that there is a great difference in the size of the chromosomes between the various samples. Although the plates shown were prepared with the same magnification, there is not enough room for the chromosomes of population sample 15 in a single plate (Plate III/6). The detailed investigation of the above-mentioned features forms one of our further tasks the results of which will be treated in subsequent papers.

Discussion

On the basis of our foregoing investigations it has been established that the chromosome number of *Scilla bifolia* populations vegetating in a state of nature in Hungary is not uniformly $2n = 18$ which would correspond to the expected diploid population. On the contrary, it exhibits variations and, moreover, differs from the data published by SOÓ (1973). According to the literature and experience it can be taken for certain that the diploid chromosome number of the species is $2n = 18$ (SATO 1935, 1942; PÓLYA 1950; GARAJOVA 1959; SIMON 1951; SPETA 1976). However, data differing from the above number are also known: $2n = 20$ (MÜLLER 1926; MEITZ 1926; DELOY 1947); $2n = 26$ (GIMENEZ-MARTIN 1959). Among the polyploid populations a great number of tetraploids ($2n = 36$) has been found by us, which is reflected in the literature the first time by SPETA who came to this result after the analysis of specimens from Austria and a number of them from Hungary. The hexaploid form has been known until recently only from the Bükk Mountains. Except for the Upper Danube Valley there is a complete areal separation between the population groups with different degree of ploidy; even in a given population the specimens were found by us to have the same number of chromosomes, which is demonstrated also by the uniform chromosome number of specimens with different morphological characters taken from the same population (Table 1, samples 6–7, 18–19 and 15–16).

As a result of karyotype analysis of diploid populations it has been established by us that even in the case of samples from different part of the country they are very similar to each other in view of both the morphology and size of their chromosomes (Plates I and III, Table 3). The identification

of homologous pairs turned to be a relatively easy task because in the great majority of cases they were placed side by side. In all cases the diploid chromosome set had a SAT-chromosome pair. This secondary construction marks the region of the formation and linkage of nucleolus (NOR = nucleolus organiser region) which on a diploid chromosome set occurs always in pairs and thus it is a permanent feature of such chromosome sets. They may be marker chromosomes as well as indicated by Austrian scientists (GREILHUBER and SPETA 1977).

Polyploidy may appear in the cells of the diploid breeding tip by means of spontaneous or induced (e.g. colchicine) doubling of chromosome number and provided that the tissues formed by this way lead to the formation of reproductive organs, by diploid gametes this change is further transmitted (VIDA 1976). This is important in our case because contrary to the diploid group which is relatively uniform, the polyploid group exhibits a very rich variety. On the basis of the investigations made hitherto, it may be assumed that the process of polyploidization took place parallel to the spreading from west to east. This is supported by the fact that in the seemingly ancient area of *S. bifolia* s. str. described by LINNÉ, i.e. in South Germany and in the Danube area of Upper Austria, there occur almost exclusively diploid populations. Hybridization plays an important role in the formation of polyploidy. From an evolutionary point of view polyploids of non-hybrid origine are called autoploids, while alloploids are stabilized interspecific hybrids.

Genetically the picture is very interesting in the upper Danube area in Hungary (Szigetköz) where diploid and polyploid occur together over a relatively small area (Plates I and III). The comparative analysis of karyotypes, together with SPETA's results (SPETA 1977), supports our suggestion that the populations vegetating along the Hungarian Section of Danube are identical with *S. vindobonensis* described by SPETA; those populating in Central and Western Transdanubia belong to the species *S. drunensis* and the populations of the Northern Central Range belong to *S. buekkensis*. Our opinion is strengthened by macromorphological differences and by the limits of their areas too. *S. vindobonensis* has ruddy leaves and stem, and dark violet-blue perigone and ovary with a sharp transition to white at the lower side. Its seeds are bright sand-coloured and elaiosomes are flattened, with pressed cylindrical shape and smooth surface. It populates mainly the wet gallery forests of hardwood along river banks in the lowlands. *S. drunensis* is stubbier than *S. vindobonensis*, with green leaves and stem, bright violet-blue perigone and ovary, and brown seeds when they are ripe. Its elaiosomes are taller, roundly cylindrical, and it populates the oak-forests with hornbeam groves in Central and Southern Transdanubia. The inflorescence of *S. buekkensis* starts at the very base of the stem with long pedicles. Its flowers are dark violet-blue and larger than that of the previous two species, seeds are brownish black and the

elaiosomes are pearly, highly pedimental. This species is found in the beech-woods of the Northern Central Ridge.

The Szigetköz area, which exhibits a great genetical variety may be considered as the gene centrum of the species *S. vindobonensis* from which the species extends in a western direction as far only as Vienna, while to the east along the Danube in a widening strip (SPETA 1976). Our planned study of meiosis are expected to answer the question of whether the process has evolved or is presently evolving in the direction of auto- or allopolyploidy. The heavy climatic changes in the Pleistocene glaciation periods over the area might play a great role in the emergence of polyploids. It seems as if the transformation of species from diploid towards polyploid groups would take place starting from a Central European centre — which has not yet been delineated exactly, maybe it is the foreground of the Alps — and continuing eastward (Fig. 1).

Regarding the spreading of this group of species Southern Transdanubia deserves special attention. Here we have found diploid variants of small stature in the mountains, while the plains are populated also by diploid populations, but these are very similar to *S. vindobonensis*, with tall stature and many flowers. The specimens collected from the Mecsek and Villány Mountains have few flowers (3–5) and bright cream-coloured seeds, nevertheless their elaiosome is slightly pearly, similarly to that of the tetraploids. Its more detailed analysis is under progress. The two populations collected in the Zemplén Mountains are morphologically different from those discussed above, in spite of the fact that they are diploid. They have darker seeds than those in *S. vindobonensis* and brighter green vegetative organs, which are very soft and fragile. In the vicinity of Doboz, Békés county, such populations have been found again in the oak-forests of the Kőrös flood area which are morphologically and karyologically similar to those along the Danube (Plate II/b). Presumably this is the easternmost area of occurrence of *S. vindobonensis*. On the basis of the facts described above it seems to be almost certain that *S. vindobonensis* is in fact an characteristic element of Pannonian flora.

In the course of specimen collecting it occurred repeatedly that homogeneous groups with a definite difference between them in their size have been found on the same site, which, however, were similar to each other in other characters. Therefore both variants have been analysed from two diploid and one tetraploid population. The identity of their chromosome set, however, indicates that the size difference can be attributed presumably to a difference in soil conditions or to other ecological factors.

Our further cytological investigations are to be devoted to a more detailed karyotype analysis of additional diploid populations and subsequently to the study of polyploid groups.

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COMPARATIVE ANATOMY OF THE ANDROECIUM OF MALE STERILE AND FERTILE SUNFLOWERS (*HELIANTHUS*)

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The comparative anatomy of male sterile (CH-0, HR-0) and male fertile (CH-3, CR-3) *Helianthus* flowers of different origin is discussed. The structure of anthers and the form of pollen grains are closely related to male sterility. Sterility is different in case of male sterile lines. Androecium is reduced in the CH-0 cytoplasmic male sterile maternal line. The anther tube is normal in the flowers of the genetic male sterile HR-0 line, the pollen grains are deformed, however.

Introduction

Male sterility has a significant impact on the production of sunflower hybrid sowing seed. At this time directed cross-pollination and cross-fertilization are not completely assured, that is the problem of producing self-incompatible lines and inducing male sterility by chemicals is not yet solved. Its primary reason is the enormous variability within sunflower populations.

Genetic (KUPCOV 1935, GUNDAYEV 1966, VOLF 1966, KOVARSKI 1966) and cytoplasmic (GUNDAYEV 1966, VOLF 1966, STOYANOVA 1967, LECLERCQ 1969, ANASCHENKO 1970) male sterility was promising for a large-scale production of sunflower hybrids.

Unfortunately, the sterility obtained from different populations of *Helianthus annuus* (GUNDAYEV 1966), the protogyn line created from the Armenian sunflower by ANASCHENKO (1969), and the c.m.s. source obtained by hybridization with *Helianthus lenticularis* proved not stable enough. Similarly, considerable lability was further observed in the male fertile line created through interspecific hybridization with *Helianthus grossoserratus* in the experiments by GEORGIEVA and TODOROVA (presented by KOVACIK-VLEKOVA 1980). Due to this problem, these products were not used in agronomical practice.

Nevertheless, the simplest case of genetic male sterility (monogenetic regulation), which is combined with a marked restoring process, proved to be useful for practical purposes. This is the alloplasmatic form obtained by LECLERCQ through hybridization of *H. annuus* and *H. petiolaris* (FRANK 1978).

However, the disadvantages of producing hybrid sowing seed using male sterility was that 50 and 75 per cent of the marked fertile individuals had to be removed by hand from the respective populations.

In addition, some fertile not-marked individuals, the so-called recombinant individuals, occur in such a population reaching a few per cent of the total. Their earliest removal is possible only at the beginning of flowering, when they become recognizable by the normal shape of anther tubes. Of course, it is doubtful whether there are intermedier male fertile individuals, that are impossible to select by eye, present in the genetically produced HR-0 male sterile maternal lines of Gahib-7, Gahib-13 and Gahib-18 (FRANK 1978), and also in the cytoplasmic

CH-0 male sterile maternal lines of Citosol-2 and Citosol-3 hybrids (FRANK 1979). It poses a problem as their presence reduces the efficiency of hybridization.

The only way to find an unambiguous solution to the above problem is a comparative anatomical study of the stamens of different male sterile and fertile flowers. Such a study may inform us about the differences between the microsporogenesis of normal and aberrant flowers. Furthermore, it may show if there is a difference among the genetically dissimilar male sterile forms with respect to phenology of flowering.

Material and methods

The samples necessary to the study of flowers and anthers were collected at the Experimental Farm of the Cereal Research Institute in Kiszombor. The flowers in the samples are similar to those regularly used in the plant-breeding work of the Institute. Most of the flowers were in the stage of stamen-maturity, the others were in that of pistil-maturity. Proterandry may be easily observed in the flowers.

In this study four types of *Helianthus* flower were examined. These are:

1. CR-3 restorer parental line
2. CH-0 cytoplasmic male sterile maternal line
3. CH-3 cytoplasmic restorer line (fertile)
4. HR-0 genetic male sterile maternal line

Special attention was directed to dissimilarities in the structure of anthers and in the development of pollen grains of male sterile and fertile flowers.

Prior to the microscopic study the flowers were fixed in ethanol containing some glycerine solution. After dehydration, the anthers were embedded in celloidine. 20–30 μm thick cuttings of the anthers at various developmental stages were prepared by microtome. The cuttings were dyed with haematoxyline, the slides were made using Canada balsam. The structure of the wall of anthers, the secondary sporogeneous cells and the exine of pollen grains were examined. About 30 cuttings per sample were evaluated.

Results

The androecium of cultivated sunflower varieties consists of 5 stamens. The anthers are grown together forming an anther tube (synandria). There are introrz stamens in the tube, that is the halves of the anthers open towards the stigma (Figs 1 and 2). This phenomenon, being observed scarcely in other species, is characteristic of the self-pollinated plants.

Results of the study of each line may be summarized as follows:

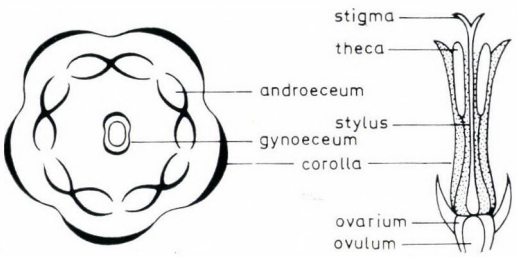

Fig. 1. Horizontal and vertical section of a *Helianthus* flower. Horizontal section at the level of anther tube. Schematic representation

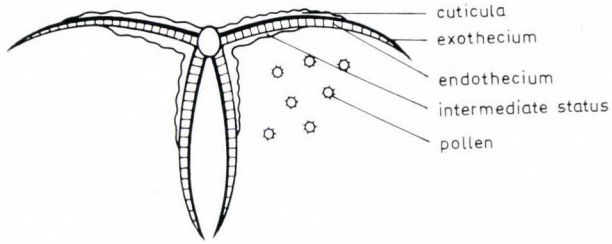

Fig. 2. Diagram showing the cross-section of an open anther

1. CR-3 restorer paternal line

Anthers covered with thick cuticle outside. Some papillae on the outer walls of exothecium. Endothecium consists of one layer of cells, the cell wall thickened with laths. The transitional and tapetum layers not visible on the open wall of anthers, the tapetum completely utilized as alimentary layer during the development of pollen. Wall of anthers thin. Pollen grains spherical, normally developed, centrifugal thickenings with papillae on their surface. Pores large, their number between 2 and 4 (Fig. 3).

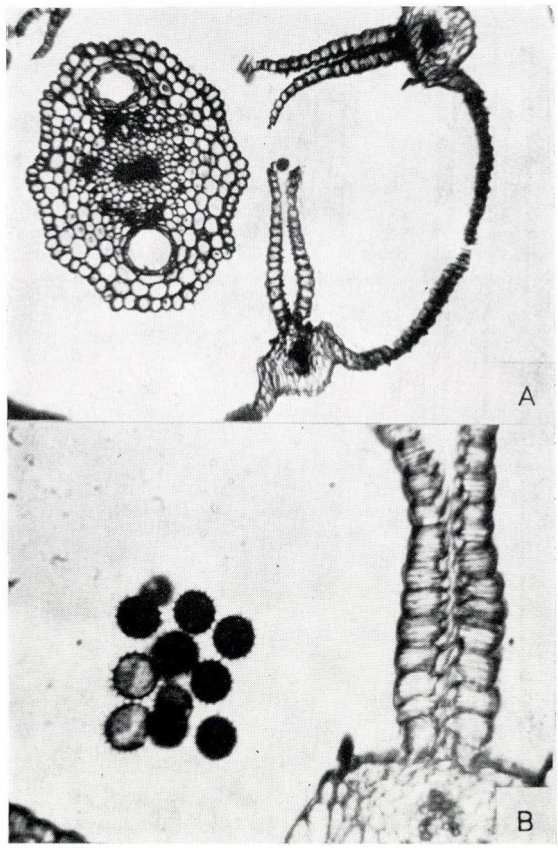

Fig. 3. CR-3 restorer parental line. A. Open anthers and the cross-section of stigma. Magnification ×110. B. Cross-section of the wall of anther whose endothecium is thickened with laths. Note the centrifugal processes on the surface of pollen grains. Magnification ×270

2. CH-0 cytoplasmic male sterile maternal line

In most flowers the whole anther tube reduced, only filament residuals occur. Of course, these flowers can produce no pollen (typical male sterility).

In flowers with anther tube still present, the wall of anthers reduced, i.e., the characteristic division of the walls of anther into four layers not seen. No thickening on the cell walls of endothecium layer, which takes part in opening the mature anther. No pollen developed in the archaeosporia of such anthers. Even a single anther with pollen was not found in the material. In conclusion, this line is typically male sterile.

It was also observed that the gynoecium of these flowers is relatively more developed than in the others (Fig. 4).

3. CH-3 cytoplasmic restorer line

Structure of flowers, anther tube and wall of anthers same as in 1 (CR-3 restorer paternal line). Many pollen grains developed in anthers. External morphology of pollen grains

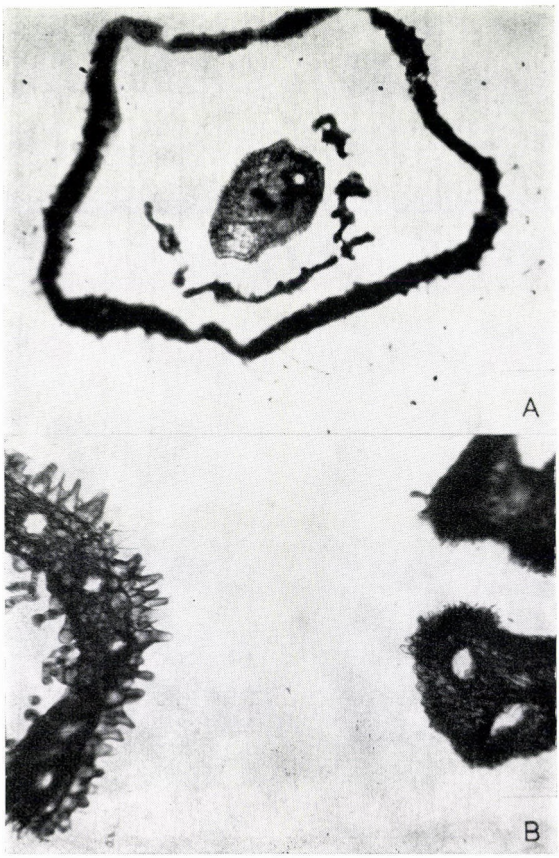

Fig. 4. CH-0 cytoplasmic male sterile maternal line. A. Androecium between the gynoecium and the petals is completely disorganised. Magnification ×50. B. No stamens developed between gynoecium and the petals, as this photograph illustrates. Magnification ×110

is normal. Pollen size 25–30 μm. Minor or major processes of intine observed on pores at several places. Flower is typically fertile (Fig. 5).

4. HR-0 genetic male sterile maternal line

Androecium normally developed outside. Walls of anthers also normal. Numerous pollen grains developed in pollen sacs. These pollen grains, however, are different in many respects from the normal pollen. Their shape variable, no dominance of spherical forms and many of them deformed. Exine of pollen grains undeveloped. No centrifugal thickenings of the cell walls of pollen, the surface of pollen grains is rather smooth. Pollen sterile, having no nucleus. This form of male sterility, i.e. when flowers yield sterile pollen, is fairly characteristic (Fig. 6).

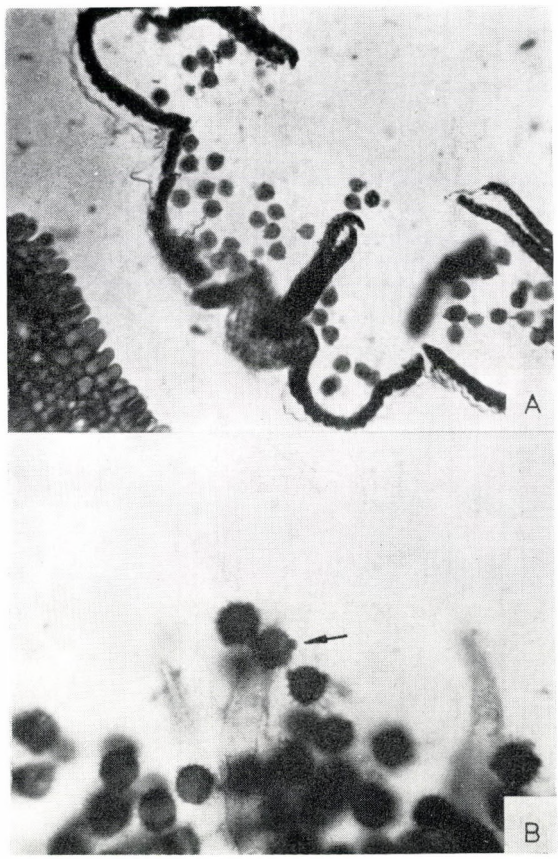

Fig. 5. CH-3 cytoplasmic restorer line. A. Cross-section of androecium. Many pollen grains seen in the anther. Magnification ×110. B. The intine of pollen grains is protruding at many places. Magnification ×270

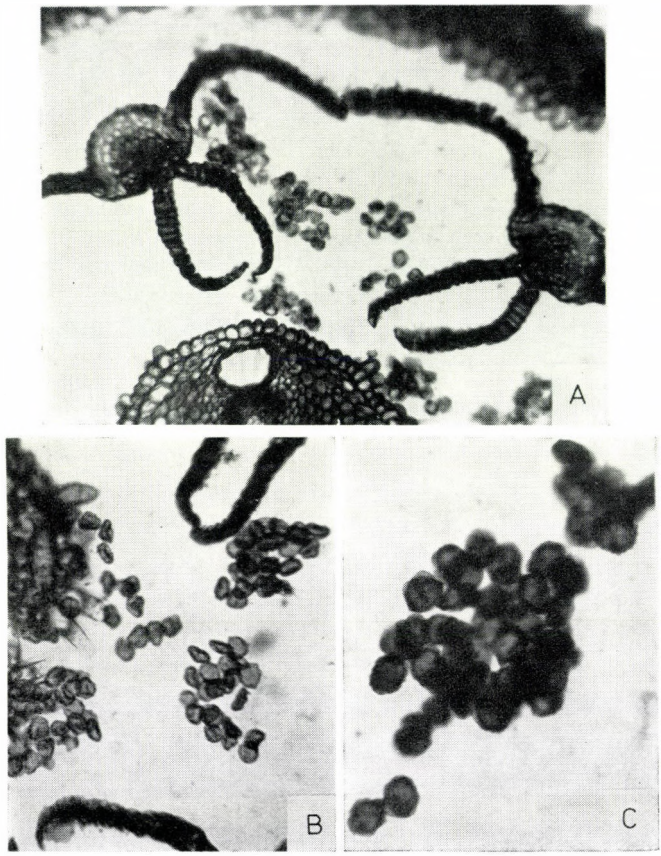

Fig. 6. HR-0 genetic male sterile maternal line. A. Cross-section of normally developed anthers. Magnification ×110. B–C. Deformed pollen grains incapable of living. No centrifugal thickness visible on their surface. Magnification ×140, ×270

Summary

1. In the different sunflower cultivars the development of androecium, the structure of anthers and the characteristics of pollen grains are closely related to male sterility.

2. Male sterility may be different depending on the morphological and anatomical features of androecium.

3. In case of cytoplasmic maternal line the anther is reduced. Even if the anther is developed, it has no pollen.

4. In the HR-0 genetic male sterile flowers the anther tube and the wall of anthers are more or less normally developed. However, they are sterile having deformed shape, reduced exine and no nucleus.

5. Two of the studied sunflower lines proved to be fertile, the others sterile.

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SPATIAL PROCESSES IN THE ANALYSIS OF VEGETATION: THEORY AND REVIEW

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This paper is concerned with the time-static spatial dynamism in the analysis of vegetation. The main objective is to provide a theoretical framework for the discussion and future use of spatial processes. A process is defined as a sequence of changes in real or abstract space associated with a vegetation survey. The different spaces also constitute a series, permitting the distinction between two basic types of processes. The primary processes are defined by the investigator. Once a primary process is defined, dependent processes are automatically generated in the subsequent spaces. Further distinction is made according to the number of controlling parameters simultaneously changed during the process. The role of different processes is investigated in real, data, resemblance, classification and ordination spaces, and in the space of derived variables. Past contributions to the topic and the task of examining spatial dynamism are reviewed.

1. Introduction

The idea of process in vegetation has usually been tied with a sequence of spontaneous changes that occur in real space and time. During succession, for instance, the replacement of one species by another and the colonization of bare areas, as a result of the reproduction, propagation, growth and competition of species, represent the spatial-temporal dynamism. In the study of vegetation, however, the surveyor is often concerned with changes in real space that are not related to time. When the characteristics of sampling or some parameters of pattern analysis are subjected to successive modifications, time-static processes are defined. Although these processes are artificial, they do reflect inherent characteristics of the plant communities being studied.

It is important to realize that the term space is not necessarily limited to real three-dimensional space. Recently the use of derived variables (e.g., diversity) and multivariate techniques has become widespread in plant ecology, therefore abstract spaces are automatically involved even if the investigator is not aware of this fact. In abstract spaces different types of changes may be defined and used. Most of these are time-static, such as data transformation and standardization, or the successive modification of controlling parameters in the algorithms of multivariate techniques.

The analysis and discussion of time-static processes in real and abstract spaces appear to be of fundamental importance for three main reasons:

(1) The development of new numerical techniques has received increased attention in recent years. The use of multivariate methods is now a daily practice, but some classical problems of phytosociological sampling has become largely ignored. As SZŐCS (1979) pointed out:

> . . . there is a striking contrast between the exactness of methods which analyze the data and the roughness of the procedures by which the vegetation is sampled. . . . the quality of sampling has influence and limiting power on the information flow in the course of a complex vegetation study.

Plot size is perhaps the best example illustrating the general situation. About 30–40 years ago, and even up to the early 70's, the relationship of plot size to different variables and population parameters (e.g., number of species, variance/mean ratio) was a fairly popular research topic. For some reason, however, the total effect of sampling conditions on the results of multivariate analyses has been neglected except in some specific aspects (KERSHAW 1961, NOY-MEIR et al. 1970, FEKETE and SZŐCS 1974, and MATTHEWS 1978, 1979).

(2) The effect of sampling design seems even more important in succession studies which involve ordination and classification. Natural vegetation changes are to be shown and assessed, but these may only be revealed by an appropriate sampling design. Consequently, the adequacy of succession studies appears doubtful if spatial processes are not taken into account. Plot size is an example. The use of permanent quadrats with fixed size is typical in recent succession surveys (see e.g,. FALINSKI 1977, VAN DER MAAREL 1980). A criticism of this practice is that the selected plot size will not always yield the maximum information to reveal successional changes (cf. JUHÁSZ-NAGY and PODANI 1983). The plot size optimal for describing the vegetation being studied may change as succession progresses. Therefore, simultaneous application of nested plots increasing in size may be appropriate. In this manner the effect of sampling at each point of time may be evaluated so that the investigator is enabled to recognize temporal changes.

(3) It is generally accepted that computer-oriented multivariate techniques are superior to the traditional methods because their results are less affected by subjective judgment. This seems, however, a self-deception, since the user of multivariate methods is also faced with arbitrary decisions. The choice of data type, transformation and standardization methods, resemblance coefficients, clustering and scaling algorithms may seriously influence the results. This effect is not always predictable even though the mathematical properties of most techniques are known. Despite the inherent objectivity of methods, the investigators' preference in favour of some particular technique will introduce much subjectivity into the survey. In this context, the evaluation of processes in abstract spaces is necessary to see how the results are affected by changes in the data and by slight modifications applied to the algorithms.

In this paper an attempt is made to establish a conceptual basis for the description and evaluation of spatial processes. First, the terminology of space, process, classification and ordination is discussed, and then the different types of processes are described. A review of the literature is embedded in the discussion in order to show existing approaches and to find their connections to the theoretical framework presented here.

2. Some basic terms

In the Introduction many technical terms were used assuming that their intuitive meanings were not doubtful. At this point, however, it is necessary to clarify the terminology concerned with spatial processes in other than the statistical sense. Terms, such as classification and ordination will also be discussed to find unambiguous definitions for later use.

2.1 Space

The Oxford Dictionary defines space as a "continuous extension viewed with or without the existence of objects within it" (FOWLER and FOWLER 1956). The most general concept of

space is topological (BAUM 1964). Since the different types of topological space are defined by axiomatic reference to relative positions of points, a space without objects is a nonsense. In a vegetation survey each methodological step is associated with a particular topological space (see WILDI and ORLÓCI 1980). The potential pathways of a study and the related spaces discussed in this section are summarized in Fig. 1. The first stage is of course concerned with the real space. The study area represents the three-dimensional physical space which may be simplified and transformed in some way to two-dimensional vegetation maps ("geometric images", SZŐCS 1979). The most critical step of the study, the sampling, may be performed on either the original or the mapped vegetation.

Abstract spaces are involved in all subsequent steps. By determining the state of each relevant variable (e.g., the number of individuals of species) for each sampling unit, the data (attribute) space is defined. Its dimensionality is potentially much higher than that of the real space. In data space the axes are variables (species) and sampling units are represented by points (species space, GITTINS 1969) or vice-versa in accordance with the attribute duality principle (LAMBERT and DALE 1964). The coordinates of points are the raw scores which are usually written in a species-by-sampling units data matrix.

Based on the use of appropriate objective functions the resemblance space is obtained in which the relative positions of points usually reflect pairwise dissimilarities, distances, etc., between the corresponding points of data space (resemblance structure, ORLÓCI 1978a), The resemblance structure of m objects is commonly expressed by an $m \times m$ matrix. If this matrix is subjected to linear decomposition, the maximal intrinsic dimensionality of resemblance space will turn out to be one less than the number of points or, if it is smaller, the number of axes in data space. A resemblance space is metric if all metric axioms (see ORLÓCI 1978a, p. 44) are satisfied. This is the case for many resemblance coefficients, but there are some exceptions. For example, two distinct points in data space are not necessarily distinguished by a chord distance (ORLÓCI 1967) in resemblance space (semi-metric space). Other functions may not fulfill the triange inequality axiom (Sørensen index) or the symmetry axiom (Kulczynski index and I-divergence information) and the resemblance space will be non-metric.

If interest lies in meaningful properties of the data other than the resemblance structure of points, a new space will result which is the "space of derived variables". Its dimensionality equals the number of derived variables encountered. The term "derived variable" is used here in the broadest sense referring to any population parameters and sample descriptors (4.2) obtained by transformation. For example, the overall characterization of data in terms

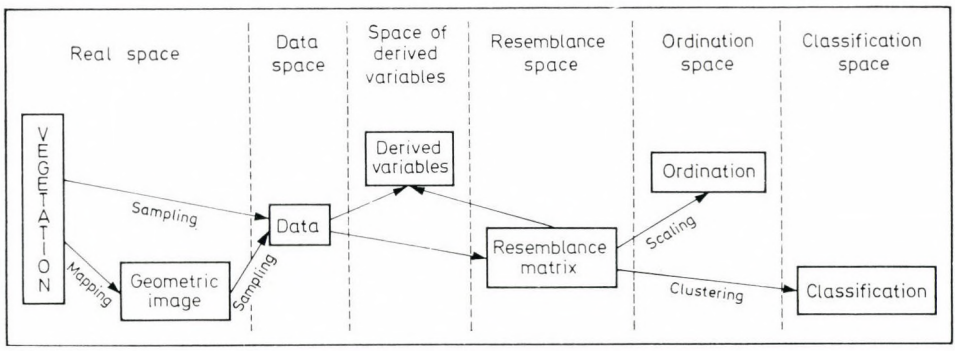

Fig. 1. Spaces and pathways in vegetation analysis

of diversity, sum of squares, expected resemblance, etc., leads to this space. The points represent data sets or subsets.

The different techniques of multivariate analysis summarize or disclose relationships among the objects in resemblance space. Scaling methods produce new coordinates transforming the objects into ordination space. If the ordination space preserves the resemblance structure, i.e., the relative positions of points remain unchanged, the dimensionality equals that of the resemblance space (e.g., principal components analysis, SEAL 1964). Some scaling methods destroy the resemblance structure in order to find a solution for an arbitrarily defined number of dimensions (e.g., multidimensional scaling, KRUSKAL 1964).

Cluster analysis produces the arrangement of points in classification space. When hierarchical relationships are established, the classification space has a maximum of m-1 dimensions and the distance of points satisfies the criteria for being ultrametric (ROHLF and SOKAL 1981) even if the resemblance space is non-metric. This is a strong argument against the use of non-metric coefficients in cluster analysis. In non-hierarchical classifications the between-group relationships are usually undefined and the intrinsic dimensionality of the classification space will be one less than the number of groups. As far as the presentation of results is concerned, the possible large dimensionality of classification space causes no problems: two dimensions are always satisfactory. Ordinations, however, cannot be shown in the plane properly since only two (or three, in case of stereograms, FEWSTER and ORLÓCI 1978) dimensions can be portrayed by a single diagram.

The discussion of conceptual spaces of plant ecology would be incomplete without mentioning the ecological space. Whereas the dimensions of ordination space are mathematical constructions, the axes of ecological space (WHITTAKER 1967) are defined as environmental gradients. Ecological space may be derived directly from the data when environmental gradients are known (gradient analysis, WHITTAKER 1967). In other situations ordinations may also lead to ecological space if ordination axes are identified as environmental gradients. Ecological space is considered as a desired output of ordination techniques (GAUCH 1982), therefore no explicit distinction will be made between ordination and ecological spaces in the sequel.

2.2 Process

The use of this term will be restricted to a series of changes strictly ordered by some internal or external criterion. A well-defined ordering is meant. A randomly or arbitrarily arranged sequence of changes is not considered a process. This restriction is consistent with the intuitive meaning of ecological processes which almost always suggest a spatio-temporal dynamism with interest focused upon events in time-domain (e.g., WATT 1947, SHUGART 1978, WHITE 1979, GRIME 1979). Succession, population growth and other changes monitored over time provide data on time series.

In spatial processes, events or changes associated with real or abstract spaces are central in importance, no matter whether time is involved or not. In statistical ecology, stochastic changes for generating spatial patterns are traditionally termed as spatial processes (BARTLETT 1975, CORMACK and ORD 1979, CLIFF and ORD 1981). For example, a completely random arrangement of points on a plane is considered to be the realization of a two-dimensional homogeneous Poisson point process (DIGGLE 1979) which develops by a series of random allocation of points in two-dimensional space. It is important that the term spatial process will be used here in a very different sense. Since pattern generating processes are not discussed here, the different terminology should not cause confusion. In the sequel, a spatial process will refer to any well defined series of spatial changes which is related to the analysis of vegetation data obtained at a given time. In this sense, the term spatial process was first used by JUHÁSZ-NAGY and his co-workers (JUHÁSZ-NAGY 1967, DÉVAI et al. 1971, JUHÁSZ-

NAGY et al. 1973). They examined association processes in space, i.e., the change of information statistical measures of interspecific relationships (see 4.2.9) as a function of sampling unit size. JUHÁSZ-NAGY's concept of spatial processes will be extended to cover many other sequences in real and abstract spaces.

Figure 1 illustrates different spaces encountered in a definite order in the course of a vegetation survey. Once a process is established in a given space, an unequivocal process will be automatically defined in subsequent spaces. When considering changes in sampling unit size, the series of plot sizes yields a series of data sets, resemblance matrices, classifications, etc. The *a priori* defined process, in the example of the increasing plot size, will be called a *primary process*. This is always artificial, the increments the sequence are selected according to design. The other processes defined automatically will be termed *dependent processes*. The change of interspecific association over plot size serves as example. It is to be noted that primary processes may also be defined in abstract spaces, for instance, specific data transformation functions applied to generate a process in data space. The primary and dependent processes will be discussed separately in sections 3 and 4.

2.3 Classification and ordination

In the general sense, classification is considered a process of allocating or ordering entities into initially undefined groups on the basis of their relationships (CORMACK 1971, EVERITT 1979, JARDINE and SIBSON 1971, ORLÓCI 1978a, SNEATH and SOKAL 1973). This should be distinguished from "identification" which is the way of assigning new, unidentified entities to previously established groups. As SNEATH and SOKAL (1973, p. 3) point out, there is some confusion over the meaning of classification in the literature:

> Classification . . . is the name of a process; however, it has also been used for the end product of this process. Thus the result of classification is a classification.

In the preceding paragraphs classification was understood in the latter sense, primarily concerned with processes other than those involved in a classificatory algorithm (i.e., a defined sequence of computational steps). To avoid possible confusions, any process leading to classifications will be called cluster analysis or clustering, and the term classification itself will be restricted to the results.

The term "ordination" was first used by GOODALL (1954). The terminological problems are analogous with that of classification. To CORMACK (1971), ordination is a process of representing entities as points in a Euclidean space. SNEATH and SOKAL (1973) define ordination as the placement of entities (operational taxonomic units, in their terminology) in an abstract space of varying dimensionality. Ordination is often used by others to mean a procedure of ordering entities along axes of variation in a one or multidimensional scheme in such a manner that this arrangement will reveal some useful information about the relationships among the entities (GREIG-SMITH 1964, POOLE 1974, VAN DER MAAREL 1979a). Furthermore, the results of component analysis, factor analysis, reciprocal averaging, that is the scaling methods, have also been frequently referred to as ordinations. The later usage will be followed which is consistent with the convention accepted for classification.

3. Primary spatial processes

The primary processes are not natural, they are artificially generated to examine some intrinsic property of the vegetation being studied or to evaluate sampling and data analytical designs. The primary processes have simple

models related to questions raised by the investigator, such as: what is the effect of the data type upon ordination? Which quadrat size might be best used to detect aggregation of individuals of a given species?, and so forth. Most primary processes are confined to the real and data space. However, they are also conceivable in the subsequent spaces of a study, where interest usually centres on the dependent processes.

The primary processes are defined by specifying the controlling parameter or parameters and the sequence of their transformations. Two basic types can be distinguished based on the number of controlling parameters: In an elementary primary process, only a single parameter is modified. In a complex process two or more independent parameters are allowed to change. When a community is sampled by a set of circular plots, whose sizes increase, an elementary process is involved. The area of the plots is the controlling parameter. GREIG-SMITH's (1952, 1964) popular pattern analysis technique exemplifies a complex process since the size and shape of blocks are simultaneously changed and these factors are independent. In this case, there is a confounding of the effects of block size and shape on, for instance, the covariance of the two species being studied (see 4.2.11 for more information).

3.1 Primary processes in real space

In classification and ordination surveys, as well as in the analysis of the spatial pattern of plant species, the most commonly used technique for data collection is quadrat or plot sampling (it is noted that terms quadrat and plot will be used interchangeably). Quadrat sampling has four basic characteristics: size, shape, number and arrangement. The successive changes in any of these parameters represent an elementary process in real space.

Quadrat sampling, as PIELOU (1977) notes, suffers from the drawback that quadrats are not "natural", but are necessarily arbitrary units, and any of the four characteristics mentioned above may have considerable impact on the findings. Since there is no general substitute for quadrat sampling in Phytosociology, it will remain the principal and most direct technique to obtain vegetation data. This fact emphasizes the importance of the study of spatial processes.

Another technique for data collection is plotless sampling (COTTAM 1947, COTTAM and CURTIS 1949), but its phytosociological applicability is limited to specific problems (e.g., the study of interspecific relationships). In plotless sampling elementary processes may also be defined by changing some parameters of the design in nearest neighbour analysis (see 3.1.5).

3.1.1 Plot size

There is a general agreement between vegetation scientists that plot size has influence on the data and results. This may be the most substantial among the four plot characteristics (CAIN and CASTRO 1959, KERSHAW 1961, 1973, NOY-MEIR et al. 1970, ORLÓCI 1978a). EVANS (1952) concluded based on a pattern study that

> . . . disagreement in the results of various authors stems in part from differences in the sizes of their quadrats, and success or failure [of their study] . . . depends upon a fortunate or unfortunate choice of quadrat size.

Later GREIG-SMITH (1964) made similar comments demonstrating that the situation did not change much since EVANS' work:

> The effect of sample size [i.e., sampling unit size] on indications of association has been largely overlooked. . . . the information derived from association data based on a single size of sample [plot] will be very incomplete and difficult to interpret.

The analysis of spatial pattern and the measurement of interspecific association are just examples, the question of adequate sampling unit size may be addressed in any other applications of sample plots in plant ecology. Estimations for population parameters (frequency, density, etc.) and their significance tests, derived variables (e.g., diversity), as well as ordinations and classifications should be treated with caution if based on a single plot size. The analysis of processes depending on the area of the sampling units may therefore contribute much to the understanding of fundamental theoretical and practical questions of sampling.

In Phytosociology, the question of adequate plot size is inevitably linked to the concept of "*minimal*" or "*characteristic*" area (cf. GOODALL 1970). The literature of minimal area is voluminous and somewhat confusing. TÜXEN (1970) published an extensive bibliography of relegant articles up to that time. It seems that minimal area could have been the sole topic of another paper. Here, only a few relevant points are made.

Almost all definitions agree in that the "true" characteristics of a community first appear at the size of minimal area and its increase does not yield significant amounts of additional information (GREIG-SMITH 1964). In general, minimal area is thought to be the smallest plot size representing the "*characteristic structure*" and composition of the plant community (CAIN and CASTRO 1959, GOODALL 1961). Differences arise in the selection of characteristics that are considered to be important in determining minimal area. WESTHOFF and VAN DER MAAREL (1973) pointed out that a sharp distinction has to be made between minimal area as a synthetic concept and the analytical minimal area. The synthetic minimal area [SMA] is defined in many ways according to the principles of different phytosociological schools, reflecting various, sometimes contradictory views. For example, the Uppsala school of DU RIETZ (1921) relied on a circular definition using constancy:

> The minimal area is that in which all the constants occur, and the constants occur in the minimal area. . . . the constants characteristic of each association [i.e., plant community type] are already noticeable in case of relatively small quadrats, while in further enlarging these the constants do not increase in number.

(TRASS and MALMER 1973). WESTHOFF (1951) gives another definition for SMA:

> . . . the minimal surface which has as a rule to be occupied by a sample of a plant community if the normal specific assemblage will be able to develop.

Without continuing with citations, it is clear that the concept of SMA is meaningful only *after* the associations or types have been established. Furthermore, it is almost always implicitly assumed that sample plots of the size of minimal area, originating from different stands assigned to the same abstract syntaxonomical unit, are relatively very similar to one another. In other words, the set of such plots has to show maximum homogeneity (in the sense of overall similarity). Consequently, if these plots are laid down within a given stand of a plant community, the sample is expected to be even more homogeneous. However, as JUHÁSZ-NAGY (1967) pointed out, it is more useful to detect an area at which the stand is found in its richest and most diverse development than to look for SMA. This area is called maximum area [MA] and JUHÁSZ-NAGY suggested information theoretical functions for its determination (see 4.2.9). MA is analogous to SMA in that it is also an *a posteriori* concept, it may be

defined for a stand which, as a complete entity, represents an already defined plant community type. For this reason, the collective term *characteristic area* [CA] may best be used.

The *analytical minimal area* is generally regarded as the "*optimal*" size of sampling units by which the vegetation should be sampled for subsequent analysis. Since this refers only to a minimal area, it seems more appropriate to use the term "*analytical characteristic area*" [ACA]. A fundamental difference between CA and ACA is that when ACA is to be determined, the vegetation types are not yet known. It is obvious that the correct recognition of types, if they exist at all, may be achieved only if the individual CAs are best approximated by ACA. Also, the sample has to show minimum overall "*homogeneity*", otherwise the differences among the possible types are not completely manifested in the data. Therefore, ACA is consistent with MA and inconsistent with SMA, indicating that MA is perhaps the more useful of these concepts in typification.

In an optimal situation, which is rather hypothetical, the CAs of the types to be recognized are equal, therefore if ACA is found, the CAs are also found and the classification is not in doubt as far as plot size is concerned. In practice, however, CA potentially differs with community types and any attempt to detect the types necessarily involves a circular argument: optimum plot size for each type can be determined only if the types are already known, but the adequate recognition of the types is conditional upon the use of sampling units of the optimum size. Moreover, if vegetation types are arbitrarily established and the CAs are determined in some way, the existence of classes could not be justified by multivariate analysis without violating the statistical assumption that plots of different size are not subjected to simultaneous scaling or cluster analysis. For these reasons, the only theoretically justifiable strategy to indicate types on the basis of their individual CAs is an iterative approach for which an example is given in 4.4.1. Fortunately, when the classifications appear less influenced by plot size, there exists a simpler alternative which does not require the determination of characteristic areas. It is discussed together with the dependent processes of the classification space (4.4.1).

Many different techniques have been suggested for pattern detection or to determine characteristic areas. All of them rest on the analysis of processes dependent on the area of plots. There are two different possibilities to modify the size of sampling units keeping in mind that the other three characteristics of sampling are held constant. These are:

1. *Nested plots.* Each plot is successively enlarged such that the largest plot will completely include k–1, the second largest k–2 plots, and so on, if k is the number of different sizes (Figs 2a–d). In this case the data and results obtained at different plot sizes are not independent from one another. This may be a disadvantage, since statistical tests for comparing results may not be valid, although the examination of dependent processes may still give useful information (e.g., cumulative species/area curves). It is not to be forgotten, however, that the nesting of plots is a prerequisite to the assessment of the effect of plot size upon, for instance, resemblance structures.

2. *Independent plots.* Each set of sample plots of a given size is laid down separately and randomly to ensure independence between plot sizes. The results can be tested for significance but the price is high: the sampling requires much more effort than the nested plots. Further difficulty is that the

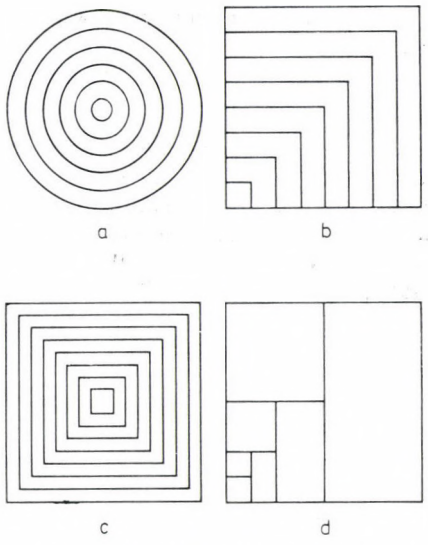

Fig. 2. Different designs for nested plots

vegetation is more disturbed or may be completely destroyed due to intensive trampling.

The smallest and largest plot size, as well as the increments are arbitrary. The choice is affected by economic considerations and one's knowledge of the vegetation to be studied.

3.1.2 Plot shape

The shape of a sampling unit may be a cause for fewer problems than plot size. Although there are some reports treating the effect of plot shape (e.g., CLAPHAM 1932, MYERS and CHAPMAN 1953, VAN DYNE et al. 1963), this problem was largely ignored. In Europe, isodiametric units have long been used. The shape is usually square since it has the great practical advantage in that the marking of plots is easily done in the field. Another reason for the preference for square-shaped units is that they can be arranged into a continuous grid (commonly used in pattern studies). Circular plots, although just as natural, are used on rare occasion in actual studies (e.g., JUHÁSZ-NAGY 1967). In North America short rectangles of 20×50 m^2 size (the so-called tenth-hectare plots), subdivided into smaller units are frequent, especially in gradient studies (cf. WHITTAKER 1973a).

In a heterogeneous vegetation the optimum plot shape depends on the objective of the survey. For classification and ordination purposes isodiametric plots are recommended; because the probability that a plot will overlap community-type boundaries (or other vegetation discontinuities) is the smallest. Therefore, it is expected that the within-plot variance (variability, heterogeneity) is kept to the minimum, whereas the between-plot variance is maximized. If precise estimates for population parameters have to be derived from the whole sample, the opposite condition is aimed at, i.e., maximum within-plot and minimum between-plot variances. This may be achieved by the use of elongated sampling units.

A spatial process with respect to shape may be the successive elongation of square plots to long rectangles or of circular plots to long ellipsoids of the same area. The elongation of shape, however, increases the boundary/area ratio thereby introducing undesirable edge

effects (GREIG-SMITH 1964). This fact has to be considered when analyzing processes depending on the elongation of sample plots.

3.1.3 Sample size

The number of sampling units is the size of the sample. This is criticial in surveys where the objective is estimation of vegetation parameters and statistical inference. The robustness of most statistical analyses against the violation of assumptions largely depends on sample size. A few plots often yield high standard error of the mean and, even if the statistical tests are significant at conventional probability levels, the confidence limits may be undesirably wide. GREIG-SMITH (1964) presents an example. The most efficient way to increase precision is to increase the number of plots, although the other three characteristics of sampling may also be changed to achieve this goal (see 4.2.2). This procedure generates an elementary process in real space. In plotless sampling the analogous process is obviously the enlargement of the sampled area.

The number of plots is closely related to sampling effort, so a balance between the precision of results and the costs involved is critical. This problem requires the study of processes depending on sample size. A starting point may be the common observation that successive equal increases in the number of plots do not yield proportional gains in the additional information. The point where the new information (or the change of results) becomes negligible may be determined by specifying the level of the desired accuracy and performing a pilot study. Of course, sample size is not just a practical question. If, for instance, the relationship between the number of plots and a derived variable is not known, the sample size has to be changed until the nature of their relationship is safely recognized.

The problem of sample size has to be treated separately in ordination and classification when the sampling units themselves are subjected to analysis. In these cases the goal is not estimation and significance testing but typification or trend seeking. There is, however, no study and consequently no evidence suggesting that the increase of sample size improves the final results. Too few plots are obviously unsatisfactory because the data will not contain sufficient information for the analysis. On the other hand, a very large number of plots will probably increase random variation (noise) which may significantly affect the results. Also, a too large data set may be difficult and too expensive to analyze even at the present advanced state of computer technology. The optimization of sample size prior to scaling and clustering therefore requires further consideration.

The influence of sample size on the stability of results obtained by multivariate techniques is to be also mentioned. One aspect of stability is the robustness of ordinations and classifications (ROHLF and SOKAL 1981) which is satisfied if the addition of new objects to the sample does not alter significantly the groups and/or trends. The robustness of phytosociological classifications and ordinations may be examined by successively increasing the number of plots analyzed and examining the resulting changes. Whereas the numerical taxonomic analogue of this problem is a central issue in systematics (cf. CROVELLO 1968), vegetation scientists largely ignore stability/sample size relationships. Although GOFF (1975) investigated the effect of the inclusion of new species on a reference ordination of other species, it seems that there are no publications in the literature concerned with the modification of sample size in multivariate analysis of vegetational plots.

3.1.4 Spatial arrangement of sampling units

The placing of plots in the field is subject to the goal of the survey and the personal experience and preference of the surveyor. In plant ecology, four different sampling designs are commonly used, the preferential, random, systematic and restricted random. Other

methods, e.g., cluster sampling, are seldom used. Before discussing the possible processes related to the arrangement of plots, it is worthwhile to summarize the main features of each sampling technique.

The traditional sampling method used frequently and mostly by European analysts is preferential. After a reconnaissance of the survey area those sites, which appear reflecting the most characteristic structure of the community, are chosen and sampled. However, as GREIG-SMITH (1964, p. 21) pointed out:

> Selection of typical sites for samples is clearly inappropriate to a quantitative approach, as their choice is dependent on the observer's preconceived ideas of the character of the vegetation, and data from such samples cannot be considered an unbiased estimate of the vegetation of the area.

Although preferential sampling is not necessarily bad, no processes can be logically defined in this method.

In simple random sampling any part of the study area has the same probability of being sampled and the placement of a plot is completely independent of the positions of those already located. The randomized arrangement ensures that the sampling is uninfluenced by arbitrary decisions; the data obtained in this way represent the most powerful input for statistical analyses. Randomness may be easily achieved by computerized sampling based on mapped and digitized data. However, the random sampling technique is less straightforward in the field if the sampled area is large.

Whereas randomization is considered the best strategy to obtain measurements for overall properties of a homogeneous vegetation, systematic sampling may provide more information on variability within an area (GREIG-SMITH 1964). In systematic sampling the plots are arranged along a regular network of points (lattice). Of the many variants of systematic sampling (see SAMPFORD 1962) the special case in which plots are placed at all points in a square lattice seems important and most widely used in vegetation studies. Term systematic sampling will be used to describe this special case. Sample size, area and inter-plot distance (spacing) are not independent in systematic sampling; and two determine the third. In many applications the plots are contiguous and they completely cover a small study area (grid). A special case is the belt-transect commonly used in pattern studies. An obvious disadvantage of this and other systematic sampling is that the position of the first lattice point determines the others, and if the whole lattice is shifted, the results obtained may be greatly different (see 4.2.11).

As an intermediate sampling method between the random and systematic methods, the use of restricted (stratified) random sampling is suggested by many authors (see SAMPFORD 1962, GREIG-SMITH 1964, GREEN 1979). This method combines the advantages of the other two sampling designs in that the study area is divided into large compartments (strata, blocks) within which the plots are placed at random. The number of plots within each block is usually proportional to its size (proportional allocation). GREIG-SMITH points out that the most advantageous variant of this strategy is obtained if the blocks are equal and relatively small in size and only one plot is laid down within each. If the number of plots to be placed within each strata is determined in such a way that the more variable blocks are sampled more intensively, a considerable increase in precision may be achieved (optimal allocation). This technique requires the knowledge of variances for each stratum. This can be determined through preliminary sampling.

It will be shown below that the objective sampling methods are in fact different stages of a series which might be termed sampling process. The process starts with the random location of a point within the study area and the determination of the other points of a lattice. In the first stage the sampling units are placed at these points as centroids (Fig. 3a) so at

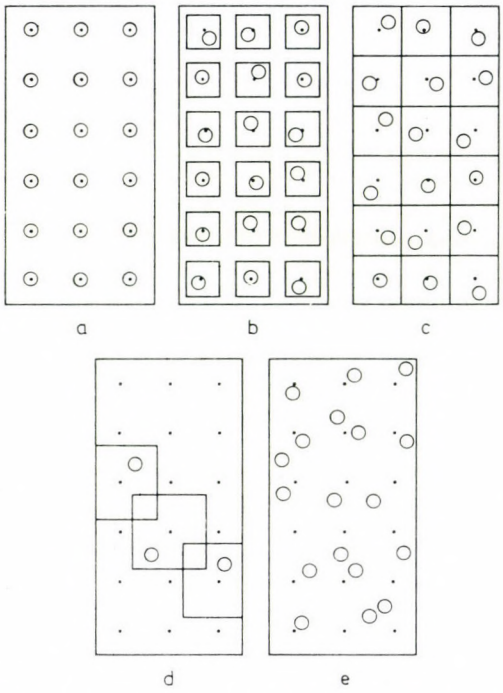

Fig. 3. Illustration of the sampling process with square compartments and circular plots. *a*: Systematic sampling. *b*: Intermediate stage. *c*: Stratified random sampling. *d*: Intermediate stage (only three strata are shown). *e*: Random sampling

this stage the sampling is systematic. In the subsequent steps the lattice points will serve as centroids of square compartments increasing in size. Within each compartment one sampling unit will be laid down randomly (Fig. 3b). When the compartments become contiguous, the design is equivalent to the most powerful variant of the restricted random sampling (Fig. 3c). The further increase of blocks results in overlapping squares, therefore the arrangement of plots will approximate more and more the randomized configuration (Fig. 3d). When all blocks become large enough to include the sampled area, the sampling units will be completely random (Fig. 3e). Obviously, the execution of this process in the field would be impractical if not impossible. Computer based sampling techniques seem to be the most efficient means for the study of the continuous series of different plot arrangements. A FORTRAN program to perform such a sampling process using digitized field data has been developed by PODANI (1982).

Another possibility for a spatial process with respect to the arrangement of sampling units is the successive increase of spacings between replicate plots (GOODALL 1961) or between cells picked up from a grid or a belt-transect (GOODALL 1974, LUDWIG and GOODALL 1978). This elementary process may be used for the detection of aggregation of individuals and possible periodicities in spatial pattern (4.2.11).

Finally, the orientation of sample plots should be also mentioned as a potential controlling parameter for a process. If anisodiametric units (strips, ellipses) are employed for sampling, and the vegetation is heterogeneous in a particular direction, the orientation of plots will obviously influence the observations. Parallel orientation with the gradient is

expected to yield more precise estimates for the vegetational variables than plots perpendicular to the gradient, since the between-plots variance is higher in the latter case (cf. LAFRANCE 1972). For this reason, the rotation of anisodiametric plots may serve as a primary process to find possible uni-directional heterogeneity within the study area. Of course, this possibility is mostly theoretical since scaling methods are more efficient in gradient analysis.

3.1.5 Nearest neighbors

The difficulties with the choice of an optimal sampling design when plots are the units, have encouraged plant ecologists to suggest the use of plotless sampling in vegetation surveys. Of the many variants of this technique (see GREIG-SMITH 1964, PIELOU 1977, for details) the method of nearest neighbors offers a possibility to define primary processes. In the simplest case the distances from randomly selected plants or random points to the closest plants are measured and analyzed. CLARK and EVANS (1954), MORISITA (1954) and THOMPSON (1956) pointed out that the method which involves measurement of the distances to the second, third, . . . , m-th nearest plant is preferred (multiple nearest neighbors). Obviously, the successive increase of m represents a primary process in real space.

WILLIAMS et al. (1969) suggested a version of multiple nearest neighbor analysis, applicable to the study of multi-species populations. The exact positions of all n individuals on the sampling area are determined and all inter-plant distances are calculated. Each plant, together with its m nearest neighbors, is then regarded as a sampling unit. The set of the n overlapping units (point-clumps) can be subjected to multivariate analysis. It was found by WILLIAMS and his co-workers that the information content of a point-clump system is entirely a function of the mean distance from the reference individuals. This fact suggests that a hybrid sampling procedure may be also appropriate in pattern studies. Each individual may be considered the centroid of a circular plot with radius r. All plants falling within this plot are then recorded, irrespective of quantity. In this sampling strategy the change of r constitutes a process.

3.1.6 Complex processes

When a simultaneous modification of two or more criteria is allowed in sampling, one has a complex primary process in real space. Clearly, the number of possibilities is large, but only one case seems important. This process is the series of block sizes implied in grid-analysis originally suggested by GREIG-SMITH (1952) and widely applied to pattern studies (see GREIG-SMITH 1964, 1979, KERSHAW 1973, and references therein). The starting situation is a grid of $2^s = 2^k * 2^{k+1}$ square units, where s and k are integers. The number of individuals, cover, or some other variable is recorded in the units. Adjacent pairs of cells are then combined to obtain 2^{s-1} oblong blocks of two units; adjacent two-unit blocks are next merged to give square, four-unit blocks, and so on. That is, whereas the blocks are doubled in size at each stage of this process, they are continually alternating in shape from a square to a short rectangle of proportion 1 : 2 (Fig. 2d). The consequences of this complexity will be discussed in 4.2.11. If the successive combinations of adjacent units lies within a belt transect (KERSHAW 1957, USHER 1969, HILL 1973a) the process is also complex with a constant block size/block length ratio. A modification of the original pattern analysis technique (FEOLI et al. 1982) may lead to an even more complex series since it allows the blocks not to be uniform in size and shape at any given stage of the process.

3.2 Primary processes in data space

The raw vegetation data may be directly subjected to numerical analysis without any change, but in most cases, simplifications and/or transformations are advantageous for dif-

ferent purposes. Data simplifications can reduce sampling effort and the costs of the survey, whereas the rationale for transformations is rather theoretical. Manipulations of the data, if the changes can be arranged into a well-defined series, are capable of generating primary processes. Four categories of these processes will be distinguished: reduction of the dimensionality of data space; changing the number of points in data space; simplification of data type; and data transformation.

3.2.1 Reduction of dimensionality

Many multivariate methods cannot be programmed and the computations cannot be performed without ensuring an easy and continuous access to the raw data during the calculations. Since the storage capacity of the computer available to the user determines maximum problem size, the analysis of some data sets may be impossible. Even if the maximum is not exceeded, some programs are very expensive to run if the number of variables is high. In some cases the computational difficulties may be diminished by reducing the dimensionality of data space. An efficient reduction may be accomplished by principal components analysis which eventually leads to an ordination space, since the original variables are replaced by independent components. However, instead of this indirect dimension-reducing procedure, relatively simple techniques which enable the user to recognize and delete the least important variables will be discussed.

It is a common observation that plant communities may be satisfactorily described based on a considerably reduced number of species. For example, AUSTIN and GREIG-SMITH (1968) concluded that ordination of rain forest communities using less than 25% of the total flora was efficient and interpretable. WEBB et al. (1967) found that a subset of large trees duplicated the original classification of sites perfectly, and no other subset possessed this property. The reason given is that the minimum information sufficient to obtain meaningful results may be provided by relatively few species, the others are redundant (KAESLER et al. 1974) and, which may be even worse, too many species may contain much noise potentially obscuring the clarity of ordinations and classifications (cf. JANCEY 1980). The subset of the best p species out of n could be chosen by examining all combinations but this method is clearly impractical in most cases (ORLÓCI 1973). A more suitable approach to this problem is the measurement of species importance (i.e., the determination of weights), a subsequent species ranking based on these values and the deletion of the less important species. The weighting and ranking procedures recently available have been reviewed by ORLÓCI (1978a), DALE and WILLIAMS (1978) and JANCEY (1979).

Species weights may be determined from the raw data only or from the data and results (*a priori* and *a posteriori* weighting, respectively). Clearly, the *a priori* weighting is now of principal concern, although *a posteriori* weighting may be also useful in an iterative approach to reduce dimensionality (and to diminish random noise, JANCEY 1980). A further categorization of weighting and ranking techniques can be made on the basis of their computational feasibility and simplicity. Some techniques require only simple examination of the data. The weight for each species is determined based on the summation of similarity values to the other $n-1$ species (e.g., MACNAUGHTON-SMITH et al. 1964), by summing the deviations from the expectations in the data matrix (DALE and WILLIAMS 1978) or by calculating the contribution of species to the total sum of squares, mutual information or other overall property of the data. Most of the weights obtained in this way will not be independent and, as a consequence, the highly correlated species will have similar ranks. This is not so with the more sophisticated ranking techniques suggested by ORLÓCI (1973, 1976a, 1978b), which may require $n-2$ algorithmic cycles to find the rank order. In the first cycle, in fact, a simple ranking is performed, the species with rank 1 is found and then removed from the data. The

second most important species will be selected in such a manner that it will be the most independent of the first, the third species will be the most independent from the first two, and so on. A rationale of this strategy is to find the minimum subset of species which accounts for the maximum variability in the data in terms of independent components. The analogy to principal component analysis is obvious, although in this case the correlations between variables are not eliminated but minimized. It is very important to note, that the ranking procedure used should be consistent with the subsequent operations. There is no point to analyze a data subset by sum of squares clustering if the species are ranked based on information theoretical criteria. However, the choice still remains subjective because the concept of sum of squares may be meaningful for several ranking methods. Therefore, an evaluation of the different strategies would be necessary by comparing their efficiency with respect to data reduction before clustering and scaling.

Having ranked the species, an arbitrary cut-off point can be specified and the less important species can be deleted. In this way a remarkable reduction of dimensionality may be achieved and the loss of information is minimized. Of course, besides ranking methods other techniques may be used to recognize unimportant variables. For example, species may be simply deleted if their cover estimate or frequency is less than a fixed value. In any case, the spatial process will be defined by changing the deletion criterion. The effect of species deletion at different thresholds upon the results can be evaluated and the point where the changes become significant can be determined.

An alternative way to reduce the number of variables is the fusion of dimensions. Phytosociological data are traditionally recorded at species level but several authors (VAN DER MAAREL 1972, DALE and CLIFFORD 1976, DALE 1977, DEL MORAL and DENTON 1977) suggest that the numerical analysis of vegetation data may be appropriate based on higher taxonomic categories. Data of species belonging to the same genus may be added or averaged, data of genera falling into the same family may also be combined in some way, and so forth. Such successive replacement of several dimensions with single ones will be a primary process in data space. PIELOU (1969) proposed a method to calculate the information content attributable to each taxonomic level. Data from preliminary sampling can be subjected to this analysis and the level where the information gain (or loss) is negligible can be determined for use in the subsequent survey.

Arguments in favour of coarse taxonomic ranks have primarily come from environmental impact studies. GREEN (1979, p. 118) gives three reasons for potential use of higher ranks. These are:

(1) Species may prove to be mixtures of several sibling species (GRASSLE and GRASSLE, 1976, provide a zoological example).

(2) The taxonomy is often poorly worked out at the species level therefore the identification at the generic level is easier and more reliable.

(3) Genera may reflect major environmental differences whereas species may be specific to the micro-environmental patchiness in a site.

The use of higher taxonomic ranks is recommended by students of environmental pollution assuming that the response of related taxa to environmental differences is similar. However, this condition is not generally satisfied. Another difficulty is that taxonomic categories are subjectively created, and the hierarchical classification of plants may be considerably different depending on the personal judgement of the taxonomist. Criteria for creating genera and higher categories may vary even within the same classification. Finally, fusion of taxonomic categories implies an underweighting of species-rich taxa which lacks theoretical justification. For these reasons, the reduction of taxonomic ranks cannot be generally recommended in Phytosociology, even though there are some successful applications in large-scale surveys (e.g., DEL MORAL and DENTON 1977).

3.2.2 Changing the number of points in data space

On first thought the proposition of changing the number of points in data space might seem to be nonsensic, since results of multivariate analyses will most likely be different and difficult to compare. However, it was already mentioned in 3.1.3 that the change of sample size may yield very useful information about the robustness of multivariate analysis. In fact, the increase of sample size can also be considered as a process defined in data space. It is a common practice to subject the species to scaling and clustering, therefore the relevance of the stability of results is not restricted to the analysis of plots. GOFF (1975) provides an example stressing that the objective of phytosociological surveys may be to establish a reference ordination of given species from a diverse region. If it is so, then, it is an important point to determine the effect of additional species upon the configuration in the initial ordination. The increase of the number of species involved represents a primary process in data space.

3.2.3 Simplification of data type

The type of data collected in the field is critical in determining the sampling effort. In classification and ordination surveys it is therefore often advisable to find a simplified data type without much loss of information. This goal may be achieved in a pilot sampling by recording the most detailed quantitative data (e.g., counts, cover). After this the effect of a series of data simplifications on the results can be evaluated, and a less costly method of data collection for which the loss of information is negligible can be selected.

When the number of individuals is recorded, the definition of an upper limit of density, k, beyond which the individuals of each species are not counted may be used to reduce sampling effort. In this case we assume that the resemblance structure of sampling units or species will not be distorted if the counting stops at k. In the pilot study the plant populations within some sample plots have to be fully censused. The amount of distortion at different values of k can be estimated after truncating the counts such that each score larger than k is set equal to k (ORLÓCI and MUKKATTU 1973).

Cover data have to be estimated as precisely as possible in the pilot study. Afterwards, the scores can be converted to categorical data in steps according to scales of diminished accuracy. Each cover datum is replaced by the mean of the cover class within which the actual value has fallen. Another possibility is the substitution for cover estimates the ranks of the corresponding cover categories. In this case, an ordinal scale will result if the categories are unequal. Such scales are commonly used in Phytosociology. The ultimate data simplification will be a presence/absence (signum) transformation for all strategies. It is to be noted that the data simplification processes imply the equalization (see 3.2.4) of variables, since the differences between high and low values of species are gradually diminished.

If one desires to analyze presence/absence, and quantitative data are available, the variables must be dichotomized. Besides the self-evident way of dichotomization in signum transformation,

$$x' = 1, \text{ if } x > 0, \text{ otherwise } x' = 0 \tag{1}$$

one can also define the dichotomy 1/0 using non-zero thresholds as suggested by NOY-MEIR et al. (1970). According to their definition a species will receive score 1 in a sampling if its quantity exceeds a given threshold. As the authors note, "it would be desirable . . . to develop a procedure which would search for an optimal threshold for each species". Such a method might help the phytosociologist not only to reduce sampling effort but also to improve the results of multivariate analyses by diminishing "noise" in the data. However, the exact relationship between noise and presence thresholds deserves further research.

3.2.4 Data transformation

Transformation of data prior to multivariate analysis is inevitable if the variables are not commensurable, i.e., they are measured on different scales with different units, such as biomass and density. Similar manipulations may be necessary if the scale is common but there are undesirably excessive differences in the range of variables, for example, species with consistently low or high cover scores. In geometric terms, data transformation is the relocation of the points in data space by means of modifying the scale on the axes. The main types of transformation are equalization and weighting (ORLÓCI 1978a).

Through equalization differences between variables are diminished by adjusting the data to zero mean and unit variance, to unit range, etc. A widely employed method of equalization is the derivation of a new range for each variable which is intermediate between the original range and unity. Logarithmic, square-root or other monotone functions may be used for the latter purpose. Weighting is the assignment of a specified weight to each variable whereby its importance is changed. The weights may be determined arbitrarily or derived from the data. The terms equalization and weighting are inseparable in the sense that equalization implies overweighting of certain variables and underweighting the others whereas weighting may imply equalization of variables which originally were not equally important.

A primary process in data space can readily be defined by the proper selection of transformation functions of the general form:

$$x' = f(x, c) \tag{2}$$

where x is the original score, x' is the new value and c is a parameter selected by the investigator. Only a few of the many possible options for (2) will be mentioned. Logarithmic and power functions, in which c is an exponential quantity, may be applied to under- or overweight dominant species to the extent specified by c. An exponential function was proposed by R. CLYMO (in VAN DER MAAREL 1979a) for the transformation of relative cover data:

$$x' = (1-\exp(-cx))/(1-\exp(-c)) \tag{3}$$

where $0 \leq x \leq 1$. For large values of c the presence/absence situation is approximated. When c is very small, x' is approximately equal to x. For large negative values of c species with high cover values are extremely overemphasized while the others are almost entirely ignored (Fig. 4). Note that this function has a singularity at $c = 0$.

3.3 Primary processes in resemblance space

It seems on first sight that a process in resemblance space could be defined in like manner as the transformation processes discussed in the previous section. That is, the resemblance function measuring distance, similarity or other relationship between objects i and j may have the form:

$$d_{ij} = f(X_i, X_j, c) \tag{4}$$

where X_i and X_j are data vectors pertaining to the respective objects and c is a parameter (or function) controlling the process. However, there appears to exist no published information, as to this author's knowledge, which treats primary processes in resemblance space. The reason may be that most resemblance functions used in ecology are not suitable to define a process. MINKOWSKI's generalized metric and RÉNYI's (1961) information of order c are obvious exceptions. The ecological meaning of the MINKOWSKI functions is not clear, however, except in two well-known forms (Manhattan metric and Euclidean distance). RÉNYI's information function can be used to generate a family of divergence measures.

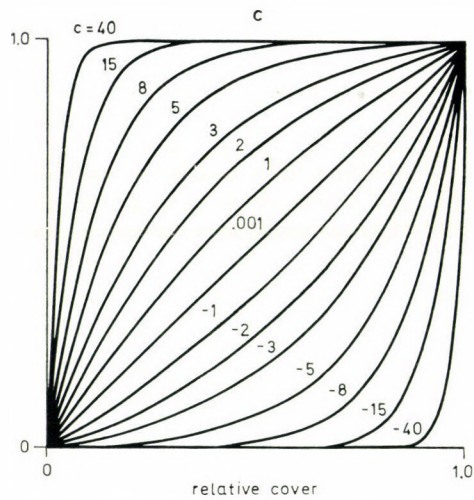

Fig. 4. Data transformation process using CLYMO's function

3.4 Primary processes in the space of derived variables

A process with respect to a derived variable, v, can be established using a function analogous to (2) and (4) given by

$$v = f(X, c) \tag{5}$$

where X is the data matrix and c represents the controlling parameter. The possibility of these processes is rather theoretical, most of the functions for derived variables are not applicable. One exception is RÉNYI's (1961) entropy of order c which might be used to define a primary diversity process. The ecological significance of changing the value of c has been studied (HILL 1973b).

3.5 Primary processes in classification and ordination space

A primary elementary process in classification and ordination space might be generated by successive small modifications of the algorithm. Of course, a number of methods are not suitable for this, since their algorithms are completely and unequivocally defined (as the majority of hierarchical clustering and the scaling methods). By contrast, in several methods one or more parameters need to be pre-determined by the user, so it is possible to set the control parameters equal to different values. All non-hierarchical clustering algorithms (JANCEY 1966, 1974, WILLIAMS and DALE 1965) and some scaling strategies (ORLÓCI 1980) are of this type. It is obvious that a great deal of arbitrariness is involved in the selection of parameters. This supports the view that the performance of these methods can only be evaluated by studying the influence of the series of algorithmic changes upon the results.

3.5.1 Hierarchical classifications

LANCE and WILLIAMS (1967) gave a common combinatorial formula to describe eight hierarchical clustering methods, defined by

$$d_{ij,k} = \alpha_i d_{ik} + \alpha_j d_{jk} + \beta d_{ij} + \gamma \left| d_{ik} - d_{jk} \right| \tag{6}$$

where $d_{ij,k}$ is the dissimilarity between group k and the group obtained with the fusion of groups i and j. d_{ij}, d_{ik} and d_{jk} are the corresponding pairwise dissimilarities (often squared Euclidean distances). The values of α, β and γ are strictly determined for seven strategies. In the eighth, the flexible sorting method, the user is faced with an arbitrary choice, and the parameters may be set to any value within the following limitations:

$$\alpha_i + \alpha_j + \beta = 1; \quad \alpha_i = \alpha_j; \quad \beta < 1; \quad \gamma = 0.$$

As β approaches 1, the analysis produces strong chaining similarly to the nearest neighbor methods. For negative values of β several well-separated and rather homogeneous clusters are obtained resembling the results of furthest neighbor sorting. There is no doubt that a series of hierarchies obtained with intermediate values is appropriate to reveal structural properties of the data.

3.5.2 Partitions

The results of non-hierarchical clustering are usually greatly affected by the selection of control parameters. In the simplest cases only a single parameter must be specified, e.g., a reallocation threshold after divisive clustering (CRAWFORD and WISHART 1968) or the number of clusters (FORGY 1965, JANCEY 1966, MACQUEEN 1967). In the latter case the dependence of results on the pre-determined parameter is obvious. In graph theory clustering, the user must make arbitrary decisions regarding the neighborhood radius by which simply or completely connected subgraphs will be obtained (ESTABROOK 1966, VAN GROENEVOUD and IHM 1974). A series of identical partitions may also be generated by intersecting single and complete linkage dendrograms at the corresponding hierarchical levels. Since any dendrogram represents a hierarchic system of partitions, all of them can be considered in a sense as graphical illustrations of non-hierarchical classification processes.

Some more sophisticated techniques (e.g., JANCEY 1974, ORLÓCI 1976b) are closely related to nearest neighbour analysis but they require the pre-determination of two or more parameters. These methods are applicable to test some *a priori* hypotheses about the existence of distinct groups (ORLÓCI 1978a). The rapid techniques aiming at the initial clustering of large data sets (JANSSEN 1975, GAUCH 1980) should be also mentioned. If only one control parameter is altered and the others are fixed, one can readily define elementary processes.

It is noteworthy that some non-hierarchical techniques do not necessarily produce unique results even if the same control parameters are applied. This is the case when the initial partition is generated arbitrarily or at random.

3.5.3 Ordinations

A primary process in ordination space can only be generated if the method requires the pre-determination of some control parameters. A good example is the procedure of parametric mapping developed by SHEPARD and CARROLL (1966). The method seeks a minimal number of dimensions (p) in which the points (representing species or relevés) are related by some response curves or surfaces which are as smooth as possible. For each predetermined value of p the VON NEUMANN quantity

$$K = \sum_i \sum \frac{(d_{ij})^\alpha}{(D_{ij})^\beta} \Big/ \left\{ \sum_i \sum_j (D_{ij})^\gamma \right\}^{-\beta/\gamma} \tag{7}$$

should be minimized, where d_{ij} and D_{ij} are the Euclidean distances between points i and j in the data and the ordination space, respectively. The parameters can have any values provided that $\gamma = \alpha - \beta$. Thus the solution depends on the specified number of dimensions and the arbitrarily determined values of α and β. As NOY-MEIR (1974) pointed out, the parameter β has a remarkable effect on the resulting ordination. The larger its value, the stronger is the weighting in favour of closely located points, therefore a local smoothness of response surfaces will be achieved. If β is rather small, a global optimum may be obtained.

Other ordination methods which should be mentioned in this context are the multidimensional scaling method proposed by KRUSKAL (1964) and a multidimensional curve-seeking procedure suggested by SNEATH (1966). Both methods have several parameters to be defined arbitrarily.

4. Dependent processes

The literature of the study of dependent processes is scattered, diverse and frequently unaccessible. Therefore any attempt to provide a complete review or just a bibliography would probably end in failure. Some specific questions have already received much attention by ecologists. For example, species/area and variance/block size relationships are very often examined regardless of the main objective of the different surveys. On the other hand, the study of dependent processes in resemblance, classification and ordination space seems less exhaustive, and there is more chance to cover all relevant work. For this reason, the following discussion will attempt to give a more balanced treatment of the topic.

The categorization of dependent processes relies on the nature of two spaces. Possibilities are shown in Table 1. Dependent processes do not exist in real space and they are of little importance in data space; their study is almost completely confined to the others.

Table 1

Possible combinations of primary and dependent processes

Space of primary processes \ Space of dependent processes	Data	Derived v.	Resemblance	Classification	Ordination
Real	+	+	+	+	+
Data	+	+	+	+	+
Derived variables		+			
Resemblance		+	+	+	+
Classification				+	
Ordination					+

4.1 Dependent processes in data space

The lowest level at which the effect of sampling design may be seen is represented by the raw scores for the variables in consideration. In the study of plant communities the most commonly used variables are cover, number of individuals (count), and biomass (yield) within sample plots. Cover is defined either as the area of the perpendicular projection of all parts of individuals of the same species onto the ground (aerial cover) or the actual basal area occupied by the plants. Absolute cover is seldom used, it is rather relativized according to the area of the sampling unit (percentage cover). The counts may also be divided by plot size to give density, the number of individuals per unit area (CURTIS and MCINTOSH 1950). The subject of this section is to study changes of these variables in course of a primary process in real space. Other vegetation variables, for example those frequently used in pattern studies (inter-plant distances, etc.), are not considered here. It is noted that the total cover and biomass of several species are derived variables and will be discussed in 4.2.1.

Most of the published work about the influence of sampling on data is devoted to the question of plot size. Early in this century, RAUNKIAER (1918) suggested that for the determination of cover the size of plots is theoretically immaterial. He considered plot size as a practical issue saying in as much as "*it is easier to estimate correctly on a small than a large area*". PENFOUND (1945), using artificial communities of randomly arranged cards, showed that percentage cover and density did not vary with plot size. In a sand-steppe community, MOLNÁR and NOSEK (1980) examined the changes of living phytomass, number of individuals and absolute cover of five species over plot size. Strongly significant linear correlations were found between each variable and the area in all cases. It might be then concluded that a homogeneous vegetation stand may be sampled by any plot size, but obviously this is not the case. Since the data are usually subjected to further analysis, the sample has to satisfy certain optimality criteria. Depending on the goal of the survey, the between and within plot variances should be minimized or maximized, costs have to be reduced or other conditions met. Therefore, the level of raw data is almost always insufficient to make correct decisions even if the assumption of linearity between variables and plot size generally existed. This problem brings up the importance of derived variables.

4.2 Dependent processes in the space of derived variables

A derived variable is usually defined as an expression combining two or more independent and direct measurements on biological material (SOKAL and ROHLF 1973). GREEN (1979) makes a distinction between four types: ratios, percentages, indices, rates, and he provides examples applicable to environmental studies. However, for the present purposes it seems reasonable to give a broader definition. Any variable which reflects meaningful properties of the data other than those expressed by the measurements themselves will be considered as a derived variable. Most of these are derived from the raw data based on arithmetic operations. The resemblance coefficients are excluded at this time, since they will be discussed separately (4.3), although in special cases derived variables may also be defined based on resemblance matrices (i.e., expected resemblance, section 4.2.10). As a consequence of this definition, total cover, number of species, mean and variance of population parameters usually not considered as derived variables will fall into this category.

4.2.1 Total cover, number of individuals, and phytomass

If interest lies in the determination of total cover, total count, and biomass of all species or a particular subset of species, and data have been recorded at the species level, the necessary information is obtained by summing the corresponding raw scores pertaining to

the same plot. There is at least one report (MOLNÁR and NOSEK 1979) suggesting that in a homogeneous vegetation stand the relationship between these derived variables and plot size is significantly linear. In other words, if these variables are relativized to unit area, no significant change will be seen. Similar conclusions were drawn by VAN DYNE et al. (1963) for production estimates of various plant groups.

4.2.2 The precision of estimates

Determination of cover, biomass per unit area and density for the whole population of a particular species is important for plant ecology and related fields (e.g., production biology, forestry, agronomy, resource inventories, etc.). These variables, especially biomass, are frequently measured for an entire species group or for all the species. The precision of estimates derived from the sample is greatly influenced by the sampling design. The optimization of sampling to achieve high precision is commonly carried out by a statistical analysis of spatial processes. Precision is expressed in terms of variance, sampling variance of the mean or its square root (standard error of the mean) and the coefficient of variation. An "*ideal*" design would give data with the least variance and would result in an unbiased estimate of the true population mean at the lowest costs. Of course, all requirements cannot be met at the same time in practice.

Intuitively, the precision of estimates at a fixed sample size is inversely related to plot size since higher proportion of the whole population is sampled by larger plots than by smaller ones. However, this relationship is also affected by the spatial pattern of species under investigation. If the population analyzed shows clumped distribution, the variance between plots would increase, and not decrease, over plot size up to the point where the plots approximately equal the mean area of clumps. Further enlargement of plots is not a guarantee of increasing precision because the variance also depends on the pattern of the clumps themselves (cf. PIELOU 1977). Therefore, one might be tempted to accept the more precise estimates obtained by very small plots, as suggested by GREEN (1979): "*the best sampling unit size generally is the smallest possible one, when sampling a given total area for an organism that has an aggregated spatial distribution*". However, if the plots are small the sample size has to be increased to reach an acceptable sampling intensity. This problem illustrates that two potential objectives of vegetation surveys, namely the precision of estimates and the detection of pattern are conflicting. Due to the aggregated spatial distribution, abnormally high variances in yield were reported by VAN DYNE et al. (1963) from sampling experiments with grasses. On the other hand, the increase of precision as a result of plot enlargement is observed in many studies for other species. VAN DYNE et al. (1963), WIEGERT (1967), THOMAS and ABOU-EL-FITTOUH (1968) and RAM BABU et al. (1981), among others, provide evidence for biomass data in economically important natural communities. FREESE (1961), O'REGAN and PALLEY (1965), O'REGAN et al. (1973), TAAFFE (1979), FOWLER and DAVIS (1979), and KULOW (1966) have drawn similar conclusions about the precision of various forest estimates (number of trees, basal area, volume of timber, etc.). According to FREESE (1961), the product of the square root of plot size and the coefficient of variation of timber measurements is approximately constant. This experimental formula gives a good fit to actual data as confirmed by TAAFFE (1979) and ZEIDE (1980). For density data O'REGAN et al. (1973) found another formula suggesting that the logarithm of variance is a quadratic function of the logarithm of plot size.

It was already mentioned in 3.1.2 that plot shape may significantly influence the precision of cover, density and biomass estimates. The problem of appropriate shape has long been a subject for investigations by agronomists and it was early recognized that long narrow units are effective in reducing the between-plot variance of yield measurements

(KALAMAKAR 1932, JUSTESEN 1932). CLAPHAM (1932) obtained the same type of results for counts of five herbaceous species in natural vegetation. HASEL (1938), BORMANN (1953) and FREESE (1961) reported that long plots were superior to squares or circles in reducing variance in forest measurements. PECHANEC and STEWART (1940) and VAN DYNE et al. (1963) evaluated the influence of shape upon plant production in different steppe communities with similar conclusions. The advantage of elongated units over isodiametric ones is due to the fact that the chance of crossing any vegetational or environmental boundaries is higher for the long sample plots. That is, between plot variances are minimized by maximizing within plot heterogeneity. Consequently, in analyzing homogeneous vegetation plot shape seems less critical, although CLAPHAM (1932) recommended the exclusive use of rectangles in Phytosociology stressing that "the soil characteristics which affect plant growth cannot be absolutely constant over an area, however small it may be". Reports on the inconsistency of plot shape with respect to precision, however, do not support the view that this factor is universally important in estimation (e.g., KULOW 1966, RAM BABU et al. 1981). Moreover, if the objective is not estimation, the use of long plots is not necessarily preferable (e.g., in the analysis of interspecific correlations, 4.3.1).

The effect of sample size upon the precision of estimates is mathematically more tractable than any other characteristic of sampling. Therefore, the intuitive feeling that the larger the sample size the higher is the precision may be easily tested. Let N denote the number of non-overlapping sample plots of a given size and shape completely covering the study area. Supposing that the sampling is free from measurement errors, the mean of a sample consisting of these N plots would be completely accurate. Let n be the number of non-overlapping and random plots actually used, and S^2_X be the variance between plots. Then the unbiased estimate of the standard error of the mean is obtained by the formula,

$$S_{\overline{X}} = \sqrt{\frac{S^2_X}{n}} \cdot \sqrt{\frac{N-n}{N-1}} \tag{8}$$

(refer to any statistical text, e.g., FREUND 1967). $S_{\overline{X}}$ should be minimized to achieve high precision. It is seen that if N is very large, the finite population correction factor, $\sqrt{\frac{N-n}{N-1}}$, becomes negligible and the value of n is decisive in determining precision. It is also obvious that decreases in standard error are proportional to the square root of n, therefore it is not worth increasing the sample size beyond a reasonable limit. Given a desired accuracy of the mean, a specified confidence interval and an estimate of S^2_X based on a pilot survey, the necessary sample size can be determined (see COCHRAN 1963, SAMPFORD 1962, GREEN 1979, for details and examples). The effect of sample size on the precision of yield estimates was studied by THOMAS and ABOU-EL-FITTOUH (1968) who suggested that increasing replication number reduces error more rapidly than increasing plot size. ROGERS (1980) made a similar survey on percent cover data and showed that the coefficient of variation was rapidly decreasing versus sample size if the plots were randomly arranged.

The relationship between the precision of estimates and the arrangement of sample plots depends on the pattern of variability within the study area. No doubt that in homogeneous vegetation simple random sampling is the obvious strategy. If heterogeneity is indicated by pilot sampling, simple random sampling is considered unsatisfactory, since it is unlikely that the different zones or strata will be proportionally represented in a random sample. Systematic sampling was first thought to be applicable to overcome this difficulty and its superiority was reported from forest studies by HASEL (1938) and FINNEY (1948). However, other reports comparing systematic and simple random sampling showed that there is little or no gain in precision (BOURDEAU 1953, KULOW 1966). In populations with periodic variation the precision

of systematic sampling is sensitive to the spacing of plots. If the sampling interval coincides with the scale of pattern the resulting variance will be extremely low because the other regions are excluded from the sample (cf. COCHRAN 1963). A smaller or larger spacing, on the other hand, may lead to much higher variance than simple random sampling, as reported by FINNEY (1950). Obviously, systematic sampling cannot be used to derive unbiased estimates of the sampling variance, and comparison to other designs is not valid on this basis. COCHRAN (1963) describes a method for objective evaluation and shows that if the variance between units is greater than the population variance, systematic sampling is expected to be more precise than is simple random sampling. This is the case if the population exhibits a linear trend, which should be very rare in natural vegetation. Therefore, another alternative to simple random sampling, namely stratified random sampling, may be more useful in diminishing sampling error. Its increased precision against the simple randomized arrangement has been demonstrated by PECHANEC and STEWART (1940) for yield and BOURDEAU (1953) for density and basal area of trees. The reason for higher precision is that systematic sampling ensures a relatively even distribution of plots within the study area. The gain in precision obtained by proportional allocation of plots depends on the difference between the stratal means: the higher the differences, the more precise is the stratified design compared to the simple random design. By definition, the optimal allocation strategy yields the highest precision, since the number of plots allocated within each stratum is determined in order to decrease the sampling error within strata. A theoretical advantage of stratified sampling is that estimates of sampling variance are valid, but difficulties may arise in delimiting vegetation strata (cf. KENKEL 1981).

The effect of spacing upon the precision of estimates is analogous to the problem of plot size/variance relationships in that the objectives of statistical estimation and pattern detection are conflicting. Whereas plot size seems equally important from both points of view, spacing received more attention in a pattern analytical context (see 4.2.11). The influence of spacing on the variance of systematically arranged plots was already discussed. The author is not aware of work examining other aspects of spacing/precision relationships.

The uniform orientation of long plots appears an important factor affecting the variance if they are arranged along a striking environmental gradient and the vegetation is assumed to be homogeneous perpendicular to it. LAFRANCE (1972) examined this problem using computer-simulated data, but the results did not verify the above statement. LAFRANCE attributed this to the relatively low length/width ratio of his plots and, following BORMANN (1953), recommended the use of more elongated units to improve precision.

4.2.3 The accuracy of estimates

In fact, the goal of any attempt to increase precision is to increase the accuracy of percent cover, density and biomass estimates. The reason that different sampling designs are evaluated on the basis of precision lies in the fact that the population means are not known. The "true" mean of a variable can be determined only by complete enumeration which is very expensive if not impossible in a large study area. Further difficulty is that several samples from the same area cannot be taken independently in the field without the effect of drastic disturbance in the vegetation. These problems render the examination of the accuracy of yield estimates all but impossible. Vegetation mapping and computer simulation of spatial pattern, however, may be used to investigate the accuracy of cover and density estimates obtained by different designs. It is always assumed in surveys that the determination of plant coordinates and cover is free from measurement error and the mean obtained for the whole area is "*true*". KULOW (1966) used maps of three different forest stands with information on tree diameter. The basal area of trees per unit area was the variable used for

comparison. Plot shape was of no consequence, and the accuracy of random and systematic sampling varied with forest type. The enlargement of plots was very efficient in reducing the deviation of estimates from the population mean. In a very different approach, LAFRANCE (1972) employed different plot shapes to estimate the mean location of species along a gradient in an artificial population. Long rectangles, both in parallel and perpendicular orientation, gave the most accurate estimates for species with aggregated pattern. For randomly arranged species, as might be expected, the plot shape was immaterial and no consistent relationship to accuracy was indicated.

4.2.4 The distribution of variables

Many statistical tests and several methods of multivariate analysis are based on the assumption that the distribution of variables is normal. Symmetric, bell-shaped distribution curves are usually accepted as good approximations to normality. For randomly dispersed populations, the symmetry of the curve of the number of quadrats versus the number of individuals per quadrat is affected by the mean which is in turn a function of plot size (cf. COTTAM et al. 1953). In aggregated populations this relationship becomes more complex. As a rule of thumb to be followed in deciding plot size, GREIG-SMITH (1964) suggested to select the smallest area which will not give more blank plots than plots with a single individual.

The distribution of cover data was first examined by WEST (1937) using basal area percentages for several species and with different quadrat sizes. The raw scores were grouped into equal cover classes (as described in 3.2.3), and the number of sampling units was plotted against percentage area for various species and plot sizes. The curves indicated that the distribution of cover class data of a common species was skewed at small plot size, whereas at large plot sizes the distribution appeared to be normal. This experiment was repeated by RICE (1967) with North American species. The skewness of the curves also disappeared and the distribution became symmetric as the plots were enlarged. However, this trend was observed for only three common species. Despite its importance, the normality of variables is hardly ever investigated in recent surveys.

4.2.5 Frequency

The frequency of a species is traditionally defined in Phytosociology as the number of plots in which it occurs, expressed as a percentage of the total number of plots examined (CURTIS and MCINTOSH 1950). In other words, it is an estimate of occupancy expected if a quadrat of the given size is placed randomly within the study site. To avoid confusions, it is noted that in statistics frequency is understood as the observed number of outcomes of a given event (in this case the number of plots in which a species occurs), but now the phytosociological terminology will be used. This concept is the source of much controversy between traditional phytosociological schools. DU RIETZ (1921) claimed that the number of species pertaining to arbitrarily established frequency classes (0–20%, 21–40%, 41–60%, 61–80%, 81–100%; the frequency distribution of RAUNKIAER) is a characteristic of a homogeneous vegetation, and plot sizes larger than the "*minimal area*" have virtually no influence on this distribution, at least within a considerably broad range (cf. BLACKMAN 1935). It was an apparent challenge for expression of opposing views since it is the homogeneity which ensures that the increase of sampling area will lead to increasing frequencies. Then, not surprisingly, WEAVER and CLEMENTS (1938) commented that "*frequency depends so much upon the size of the quadrat employed as to be without value by itself*". PENFOUND (1945) concluded from the study of artificial populations that frequencies and the number of species in the frequency classes of RAUNKIAER vary with quadrat size. CURTIS and MCINTOSH (1950) examined the relationship among frequency, density and plot size in a simulated community and demon-

strated that frequency increases more rapidly with increasing quadrat size when densities are great than when densities are low. The shape of RAUNKIAER's frequency distribution curve was markedly affected by plot size. The authors concluded that a RAUNKIAER distribution is of no value in indicating homogeneity of a community, and may be interpreted only with reference to quadrat size and density. GREIG-SMITH (1964) pointed out that frequency also depends on the spatial pattern of species. He examined the theoretical influence of sample size on frequency estimates, and demonstrated that the confidence limits for frequency values are too broad if the estimate is drawn from a small sample. As an obvious remedy to this, the use of very large sample size was recommended. In view of the contemporary vegetation studies the debate over the validity of frequencies seems fairly sterile, although species frequency estimates are still used as input data for information analysis (e.g., WILLIAMS et al. 1969, JUHÁSZ-NAGY 1976, etc.), and not without success.

A relative frequency of a species is obtained by dividing its frequency by the total of the frequency values for all species. CURTIS and MCINTOSH (1950) illustrated that in a homogeneous simulated population the relative frequencies approach the value of $100/n$ (n is the number of species) as plot size increases. In fact, this result was obtained independently in the florula diversity surveys of field data by JUHÁSZ-NAGY and PODANI (1983), where zero florula diversity implies equal relative frequencies. This is the result if all species are present in all sample plots (see 4.2.9).

4.2.6 Relative density

This quantity is the percentage of the total number of individuals of a species relative to the total of all species. By definition, this is the estimated probability that a randomly selected individual belongs to this species. CURTIS and MCINTOSH (1950) showed that relative density is largely independent of plot size. The accuracy of the estimate in random populations, however, proved to be subject to plot size and sample size in another study of simulated populations (COTTAM et al. 1953). It was demonstrated that accuracy is in fact a function of the number of individuals enumerated in the sample. This is of primary consequence in the species/individual diversity surveys to be discussed in 4.2.8.

4.2.7 The number of species

The relationship between species number and area has been the subject of numerous studies in various fields of biology. In Phytosociology, fundamental ideas of different schools are based on the examination of species/area curves. Before turning to these concepts it is mentioned that a potential source of difference in interpretations is that there is no unified data collection method for species/area curves. Two basic strategies may be used (cf. GREIG-SMITH 1964, PIELOU 1977):

1. *A "true" species/area curve* is derived from a series of samples in which every sample plot is assumed to be independently allocated, regardless the size of the others. Data for each plot size are then screened and the mean number of species per quadrat is calculated. The estimates of the mean are unbiased since the design is completely random. This ideal strategy seldom occurs in actual studies (e.g., HALL and OKALI 1979).

2. *Cumulative curves* ("*collector's curves*", PIELOU 1977) are obtained based on either a nested design or by increasing sample size. In this case data for different plot sizes are not independent, a rare species occurring in one of the smallest or the first plots by chance will necessarily be present in all samples. Although interdependence may be a drawback from a statistical point of view, this method is generally used. Most functions of the type,

$$S = a + b \log x \tag{9}$$

where S is the number of species and x denotes area, suggested by several authors (see GREIG-SMITH 1964, for details and references) are in fact approximations to cumulative curves. Other formulae (e.g., KILBURN's function, see below) were also inferred from a nested design. PIELOU (1977) discussed the relationship between species-abundance distributions and cumulative species/area curves with relevant conclusions regarding the homogeneity of the community sampled. However, as PIELOU herself discovered, species/area curves from plant communities cannot be interpreted in practice. The assumptions of the existence of a log-series or a negative binomial distribution for plants are usually not satisfied (PIELOU 1977). Further difficulty is that plant individuals cannot be distinguished in case of many species (e.g., grasses).

The relation of species number to sampled area has been investigated with much effort but apparently with little success. There were many attempts to develop a method capable of selecting a particular point on the curve or on the area axis and thereby determine a characteristic area. The minimal area concept by BRAUN-BLANQUET (1951) relies on the statement that the $S : x$ curves level off at a given plot size, but this is not always expected to happen in view of more recent studies (cf. KILBURN 1966). HOPKINS (1955) examined several communities and found that the $S : x$ curve was roughly linear for large quadrats. He suggested to use the interception of the projected linear segment and the area axis to determine an "*objectively defined area of the community*". KILBURN (1966) proposed a "*power function*" which appeared to give a good fit to the actual data and suggested its first derivative as an objective technique to find optimum plot size. Other, more or less arbitrary techniques are reviewed by CAIN and CASTRO (1959), GREIG-SMITH (1964) and bibliographed by TÜXEN (1970). There is no doubt that species/area curves may reflect important intrinsic properties of plant communities but it appears that their use to find characteristic areas for further analysis is not theoretically justifiable. The "*objective*" area obtained by HOPKINS' method was always too small to be biologically significant whereas KILBURN's technique involves an arbitrary selection of "*appropriate slope values*". However, the fundamental problem with the species/area curve as a basis for optimum plot size determination is that the optimum differs with the purpose of the study. It is sufficient to recall the contradictory objectives of estimation and typification. The optimum has to be found by a technique compatible with subsequent aims and operations. Manipulations with species/area curves cannot satisfy all requirements.

The shape and arrangement of sample plots have been little investigated in this context. These factors have probably no practical influence on the observed species number even in a species rich community if a reasonably large plot and sample size is used. It may be assumed, that very long but small plots are more likely to contain more species than isodiametric ones of the same size (cf. NOSEK 1976). If the sample size is small, the systematic and stratified random designs are expected to indicate more species than a simple random arrangement.

4.2.8 Species/individual diversity and evenness

In the past two decades diversity indices were among the most widely used mathematical tools applied to ecological studies. Whereas the discussion of the many available formulae and the criticism of the popular concepts of diversity is beyond the scope of the present work, reference is made to PEET (1974), PIELOU (1975) and GREEN (1979) for exhaustive treatments. The subsequent text discusses the spatial aspects in the way that these relate to the measurement of diversity and evenness.

The diversity of a multi-species population is a function of species number and the number of individuals belonging to each species. In a fully censused population the diversity is exactly known, supposing that there is no error in the counts. If complete enumeration is

impossible, as it is in most surveys, the diversity is estimated from a sample. Clearly, the estimation of the number of species and the relative density of each is improved by increasing the number of individuals in the sample (cf. 4.2.6–7), therefore the same effect is expected for diversity. Consequently, the increase of plot and/or sample size is an efficient way to improve precision. This is illustrated by WOLDA's (1981) simulated experiment in which the standard deviation of diversity estimates obtained by replicate samples decreased as sample size increased. The shape and arrangement of plots do not appear important unless the total sampled area is small.

Empirical results (e.g., HEYER and BERVEN 1973, NOSEK 1976, FEKETE and KOVÁCS 1978) suggest that the curve of diversity estimates versus sampled area (sample or plot size) first increases rapidly, but not necessarily monotonically, as it is approaching the "*true*" diversity of the community. At large sampled areas the estimates are slightly oscillating and no upward trend can be seen. Diversity curve may serve as a basis for estimating diversity in terms of SHANNON's entropy, as described by PIELOU (1975). The relationship among sample size, diversity, and underlying spatial arrangements of species was examined by KOBAYASHI (1981), using simulated data. He showed that some of the parametric diversity indices were markedly influenced by sample size depending on the spatial distribution. Shannon's entropy seemed to be the least dependent on sample size regardless the type of distribution.

The concept of species evenness is closely related to diversity. By definition, the evenness of a community is maximal if all species are equal in abundance and minimal if all but one species are represented by a single individual. Simulations and examinations of real data (e.g., NOSEK 1976, KOBAYASHI 1981) demonstrated that species evenness tends to decrease as the sampled area increases. This is purely a mathematical fact without a biological basis, if the number of species increases at the same time (cf. PIELOU 1975). In other words, evenness estimates derived from a sample are usually overestimates of the "*true*" population value. Therefore species evenness appears of no theoretical and practical significance unless the species number of the community is known (PEET 1974, PIELOU 1975). Contrary to animal populations, the determination of species number is not necessarily an impossible task in terrestrial plant communities. The real difficulty with diversity and evenness measurements in vegetation studies is that plant individuals are not always distinguishable.

4.2.9 Supraindividual diversity

In the analysis of the vegetation, a fundamental problem is to determine the spatial variation of a community over an area or an environmental gradient. Species/individual diversity is completely uninformative in this respect for obvious reasons. A more adequate approach is due to JUHÁSZ-NAGY (1967, 1976) who suggested the use of SHANNON's entropy function to measure the diversity of a sample on the basis of the species composition of each plot. Since the basic unit is not the individual but a collection of individuals (i.e., those present in a quadrat) this kind of diversity is generally termed supraindividual diversity (in case of plant communities it is called florula diversity, cf. JUHÁSZ-NAGY and PODANI 1983). A substantial difference between this and species/individual diversity is that the spatial dependence of supraindividual diversity is not simply the matter of estimation.

The florula diversity of a sample consisting of m plots is given by,

$$m\hat{H}(A, B, \ldots, S) = m \log m - \sum_{k=1}^{2^s}{}' f_k \log f_k \qquad (10)$$

where $A, B, \ldots, S$ symbolize species, s is the number of species and f_k is the number of quadrats with the kth species combination (florula). Note that 2^s different species combinations are possible including the one containing no species ("*empty*" *florula*). It is assumed that the plots follow a random arrangement.

There is evidence in the literature (see the references made in this section) that quantity (10) first increases and then decreases if plot size is increased. The plot size where the maximum is obtained is characteristic of the community and is termed the "*maximum area*" (JUHÁSZ-NAGY and PODANI 1983). The maximum does not necessarily imply that all the 2^S potential florulas may be manifested in the sample, since most theoretical combinations cannot occur due to the non-random ground pattern of species. By the same reasoning, some particular combinations will be more likely to occur than others. At a much larger plot size florula diversity becomes 0, this is the "*minimum area*" in terms of florula diversity.

It can be shown that (10) is in fact the joint entropy of the species:

$$m\hat{H}(A, B, \ldots, S) = m\hat{H}(L) - m\hat{I}(A, B, \ldots, S) \tag{11}$$

where $m\hat{H}(L)$ denotes the estimate of the local distinctiveness of species ("*total information*", ORLÓCI 1969, SNEATH and SOKAL 1973, "*information content*", WILLIAMS et al. 1969) and $m\hat{I}(A, B, \ldots, S)$ is the estimate of association (or mutual information) among species. These functions also have maxima, indicating two other characteristic areas, namely the compensatory area and the area of maximum associatum, respectively (see JUHÁSZ-NAGY and PODANI 1983, for more details).

Supraindividual diversity and related characteristic functions have also been applied to crustacean plankton assemblages ("*faunal diversity*", DÉVAI et al. 1971, JUHÁSZ-NAGY et al. 1973). The changes of these functions during succession were studied by JUHÁSZ-NAGY and PODANI (1983). Local distinctiveness only was measured by WILLIAMS et al. (1969) at various clump sizes in multiple nearest neighbor analysis (3.1.5). The extension of these studies to many other community types would be desirable in order to provide further information on characteristic functions as to their potential use in optimizing plot size.

4.2.10 Expected resemblance

Additional information about spatial variability in a community is conveyed by the expected resemblance (similarity or dissimilarity between two random plots). An expectation can be obtained in terms of the non-diagonal elements (d_{jk}) in a resemblance matrix,

$$E(d_{jk}) = 2 \sum_{j=1}^{m-1} \sum_{k=j+1}^{m} d_{ik}/(m^2 - m) \tag{12}$$

Since the values of the resemblance matrix are not independent, one satisfactory but laborious procedure to estimate the expectation would be repeated sampling based on random pairs of quadrats. Clearly, the expected value is subject to change as plot size is modified. Several past attempts have been made to find characteristic areas on the basis of the spatial dependence of expected resemblance. GOUNOT and CALLÉJA (1962) found that the mean similarity of sample plots first rapidly and the slowly increases as plot size increases, whereas the variance of similarities is decreasing. They defined the minimal area of the community as the smallest plot size at which the expectation significantly exceeds a "*given value*". GOUNOT (1969) claimed that once the plot size corresponding to this minimal area is reached, the mean similarity cannot rise any more. MORAVEC (1973) applied SØRENSEN's coefficient to find the minimal area of different communities with varying results. For meadow data, the curve of mean similarity versus plot size appeared asymptotic, at least within the range of the plot sizes used. In two cases, however, the expectations did not show consistent trend, the slight changes were probably due to random variation. For one community, the results were even more different, and the curve showed two striking peaks. The highest value was obtained at

a very small plot size (0.25 m^2), the other maximum occurred at 100 m^2. These two maxima clearly indicated two different scales of pattern, corresponding to the understory vegetation and the tree-layer, respectively. In fact, MORAVEC's study did not verify GOUNOT's general statement and it appears that the relationship between plot size and expected similarity is a more complex one than earlier thought. This statement is supported by DIETVORST et al. (1982) who suggested to consider not only binary data but also quantitative scores and dominance relations in determining minimal area. However, the concept of an arbitrary lower bound of similarity was adopted in two of the three different situations they recognized.

At first glance the approach of expected resemblance based on the similarity of binary data, and the concept of florula diversity seem contradictory. The definition of minimum area (4.2.9) implies that the expected similarity is maximum at the minimum area, but this plot size was not reached in the studies by GOUNOT, CALLÉJA and MORAVEC. It is obvious, then, that the "*minimal area*" in terms of expected resemblance is much smaller than the minimum area of florula diversity. The area of maximum florula diversity, however, does not necessarily imply that the expected similarity is minimum at this point, since florula diversity does not reflect direct inter-plot similarities. The simultaneous application of the two methods to the same set of data would be desirable to clarify the relationship between them.

4.2.11 Pattern

The previous two sections have already touched on the problem of spatial pattern The objective in examining florula diversity and expected resemblance is in fact the analysis of multi-species pattern on the basis of the qualitative description of vegetational plots. This section is devoted to a much more elaborated topic, the study of the spatial pattern of a single species. There are two fundamentally different approaches to this: the quadrat method and the distance method of plotless sampling. The subsequent discussions are primarily concerned with the first approach.

The analysis of plant pattern by the quadrat method has been the subject of many investigations in past decades. The fundamental question addressed is whether the ground dispersion of individuals can be regarded as random, or if not, aggregated (contagious, cf. PIELOU 1977, p. 117) or regular. Various measures of the departure from randomness have been suggested, these are discussed in detail by GREIG-SMITH (1964) and PIELOU (1977). ROGERS (1974) provides a monograph on the statistical analysis of spatial dispersion by quadrat methods.

In a randomly dispersed population the expected underlying distribution of the number of individuals per plot is Poisson, regardless the plot size. Consequently, the suitably chosen measures (e.g., goodness of fit to the Poisson series, variance : mean ratio) are also independent of plot size. If the measures indicate no significant departure from the random dispersion over a wide range of quadrat sizes, the hypothesis of randomness may be accepted. In natural vegetation, however, randomness seldom occurs (cf. GOODALL 1974), although it is commonly assumed for rare species. As GREIG-SMITH (1964) points out, this conclusion may stem in part from the inappropriateness of quadrat and sample sizes used and the results should not be accepted without reservations.

If the spatial dispersion of plant individuals is non-random, the measures of the departure from randomness will not be independent of plot size (although PIELOU 1977, lists two special types of pattern for which this statement does not generally hold true). In a regularly dispersed population very small plots may fail to detect non-randomness, but this problem may be easily overcome. The variance : mean ratio tends to detect more apparent regularity as plot size increases (cf. CURTIS and MCINTOSH 1950, GREIG-SMITH 1964) if the spatial dispersion is actually regular. It is to be noted, however, that this question is rather

theoretical, since there is no good evidence about the existence of two-dimensional regular pattern in natural populations. The dispersion of desert shrubs was generally thought to be approximately regular, but a recent survey (EBERT and MCMASTER 1981) showed that this conclusion is false.

The overwhelming majority of plant species show contagious spatial distribution, where the individuals are aggregated into clumps as a result of vegetative propagation, environmental heterogeneities or spatial exclusion by other species. In this case the sampling unit size is most crucial, the dispersion may appear random at very small and regular at large quadrats, whereas significant aggregation is detected at intermediate sizes (see the example by KERSHAW 1973, p. 136). Consequently, it seems that the most admissible strategy in the analysis of aggregated populations is a sampling with various plot sizes followed by the examination of dependent processes. The various indices, as mere descriptors of pattern, may be plotted against quadrat size. The shape of the resulting graph provides some useful information about the spatial dispersion of individuals. The point(s) corresponding to the scale of pattern (mean area of clumps, etc.) are indicated by peak(s) which may be readily recognized. The troughs on the graph may be as informative as the peaks, they are indicators of regularity (see e.g., RIPLEY 1978). Theoretically, the use of independent random plots would represent the most satisfactory sampling design, since the results pertaining to each plot size could be compared by statistical tests. The second best strategy would be random sampling by nested plots (Fig. 2a–d), although the possibility of testing significance is lost. In practice, however, the use of grids and transects of contiguous quadrats has become widespread in ecology, since randomization and, especially, repeated sampling with various plot sizes is exceedingly time-consuming and the vegetation becomes more and more trampled as the sampling proceeds. The advantage of systematic sampling lies in the fact that counts of the number of individuals, cover estimates or the weight of clippings have to be determined only one time for each unit, and increasing "quadrat" sizes are obtained by combining these data in some regular way.

A technique of pattern analysis utilizing the information collected from a grid of contiguous quadrats was suggested by GREIG-SMITH (1952) and is commonly referred to as "grid analysis". The fusion strategy of this method to obtain enlarged "quadrats" was already discussed in 3.1.6. The mean square among the m grid cells is examined by a nested analysis of variance. The total sum of squares is apportioned into independent components that derive from the difference between each pair of quadrats within the two-unit blocks, from the difference between each pair of oblong, two-celled blocks within the four-unit blocks, and so forth. The sum of squares specific to blocks consisting of r units is

$$SSQ_r = \frac{1}{r} \sum_{i=1}^{m/r} x_{i(r)} - \frac{1}{2r} \sum_{i=1}^{m/2r} x_{i(2r)} \tag{13}$$

where $x_{i(r)}$ and $x_{i(2r)}$ are the number of individuals in block i of the respective size. The corresponding mean square is

$$MS_r = 2rSSQ_r/m \,. \tag{14}$$

Assuming a random distribution of individuals, each mean square is an estimate of the variance of the Poisson distribution for the counts in the grid units. Then, the ratio of mean square/overall mean is approximately 1 for each block size. If the dispersion of individuals is aggregated, MS and, consequently, the variance/overall mean ratio will increase until a block size is reached which approximately equals the mean area of the clumps. If the clumps themselves are regularly dispersed, MS will fall as the blocks are further enlarged, but if the clumps show a random arrangement the mean square will remain about the same level. Two or more peaks

may occur if the individuals are dispersed in a hierarchy of clumps. The same technique may be applied to cover data (KERSHAW 1957) or biomass (MORTON 1974).

The increase of plot size in grid analysis implies a complex primary process (cf. 3.1.6), and the simultaneous change of shape and size may give rise to confounding effects in dependent processes. It is sometimes observed that the graph of MS versus block size has a sawtoothed shape because oblong blocks consistently give mean squares less than those of the neighboring square blocks in the sequence of sizes (PIELOU 1977). Due to the alternating shape of blocks, the center-to-center distance between them is not changed when square blocks are combined into oblong ones, and this fact alone may lead to increasing mean squares in a non-uniform population (GOODALL 1963). Therefore, instead of fusing adjacent blocks, GOODALL (1974) suggested to use the center-to-center distance as conditioning parameter in pattern analysis. Random pairs of quadrats with various distances apart are picked up from the grid without replacement and the specific variances are plotted against quadrat spacing. This technique overcomes the difficulty of the dependence of successive mean squares, and standard statistical methods can be used to test whether a significant difference exists between two spacings.

Other modifications to GREIG-SMITH's grid analysis are due to ORLÓCI (1971) and ZAHL (1974). ORLÓCI used the minimum discrimination information statistic to measure the departure from a perfiect regularity (see also FEOLI et al. 1982). Confidence limits were experimentally derived to examine whether a pattern is contagious or random. Zahl adopted SCHAFFÉ's S-method of multiple comparisons in estimating the size of patches. This technique requires the use of overlapping blocks. Spatial autocorrelation (CLIFF and ORD 1981) was first applied to the analysis of plant pattern by CHESSEL (1981) and GLOAGUEN and GAUTIER (1981).

KERSHAW (1957) recognized that the orientation of the oblong blocks from the grid units may considerably influence the shape of the graph of mean squares, if the mosaic patches are not isodiametric. Despite this problem, long transects of quadrats are more commonly used in pattern analysis than two-dimensional grids. Clearly, the results obtained by these two different means are not expected to be the same, since the transect method is capable of detecting only one-dimensional spatial pattern. The use of transects is therefore recommended only in case if there is a good reason in selecting a particular orientation. GREIG-SMITH's or ORLÓCI's technique can be used, but they are probably very sensitive to the starting position of the transect (cf. USHER 1969). To avoid this, many variants of the original method have been developed (HILL 1973a, LUDWIG and GOODALL 1978, FEOLI et al. 1982). The paired quadrat-variance method suggested by LUDWIG and GOODALL is based on all possible pairs of quadrats to estimate the variance at each spacing. This method is actually equivalent to the correlogram used in time-series analysis. A recent comparison and review of the quadrat-variance techniques is due to LUDWIG (1979). Repetitive one-dimensional patterns can be detected by the paired-quadrat variance method or spectral analysis (e.g., HILL 1973a, USHER 1975, RIPLEY 1978).

4.3 Dependent processes in resemblance space

Changes in resemblance space are examined considering a primary process defined in either real or in data space. The study may be restricted to a pair of objects (species or quadrats) in which case the dependence of resemblance upon the primary process is simply demonstrated by a profile diagram (e.g., AUSTIN 1968). If all possible pairs of objects are considered, the illustration becomes more difficult and the use of plexus diagrams may be appropriate (MCINTOSH 1973). A plexus diagram is undirected and coloured, but not necessarily a connected graph in which vertices represent objects (usually species, e.g., AGNEW 1961). Two vertices are linked by an edge of colour c_l if the resemblance between the corresponding

objects exceeds the threshold t or, if an appropriate statistic is significant at probability level t. A series of such plexus diagrams may sufficiently illustrate an association process of species in resemblance space (e.g., FEKETE and SZUJKÓ-LACZA 1973, MATTHEWS 1978). A more adequate approach is the comparison of resemblance matrices by elements to express the similarity of two matrices by a single number. The use of product-moment correlation coefficient, as a similarity index and not a statistic, was suggested by SOKAL and ROHLF (1962) for this purpose. Since then matrix correlation has been widely used by taxonomists (cf. ROHLF and SOKAL 1981) but the number of ecological applications is limited (e.g. ORLÓCI and MUKKATTU 1973, see below).

4.3.1 Resemblance between species

It is often emphasized by plant ecologists that interspecific association is greatly affected by the size of sample plots. GREIG-SMITH (1964) warned that the interpretation of interspecific associations is difficult if the analysis is based on a single plot size. It seems, however, that the use of various plot sizes does not necessarily facilitate the assessment of interspecific associations. GREIG-SMITH himself pointed out that there are at least four possible causes of the dependence of associations upon plot size. Accordingly, it is not always known what causes can be accounted for by the changes.

As yet, plot shape and arrangement have not been investigated in this respect. It is easily seen, however, that isodiametric units give the most acceptable results since elongated units may indicate positive correlation between two species that are actually far apart in the field. In a heterogeneous area stratified random sampling is expected to give more reliable indication of interspecific associations than a simple random design. In this case the proportional allocation of plots is an extremely important condition. Intensive sampling within a given stratum, from which the species considered are missing, may indicate abnormally high positive associations (BRAY 1956, gave an example).

An interesting approach by NOY-MEIR (1971) should be mentioned. He explored the effect of quadrat size on the ratio of qualitative and quantitative components in the correlation matrix of species. It was found that the larger the quadrat size, the more important is the quantitative component in the resemblance matrix.

4.3.2 Resemblance of quadrats

ORLÓCI and MUKKATTU (1973) presented two examples for the use of matrix correlation in ecology. They investigated the effect of species number and individual count limit (3.2.3) on the resemblance structure of quadrats. Resemblance matrices were calculated using the most complete data as well as using simplified data sets. The amount of distortion was determined by comparison with the initial matrices. These processes were illustrated by stress profiles. The authors found that the loss of information was negligible if 40% of the species were deleted, and, if the individuals were not counted beyond 100.

4.4 Dependent processes in classification and ordination space

From a phytosociological point of view, the purpose of the analysis of various dependent processes in other spaces is in fact to find optimum sampling characteristics and data type for an adequate study and description of vegetation. Then, the main question is to what extent are the classifications and ordinations of phytosociological entities influenced by different primary processes? Past attempts to find an answer are not by far commensurable with the importance of this problem.

4.4.1 The effect of sampling

The first study on the influence of plot size upon hierarchical classifications is undoubtedly due to KERSHAW (1961) who performed normal association analysis based on two quadrat sizes. He found that three species were constant of the first four divisive species. The lower divisions were rather unstable. NOY-MEIR et al. (1970) made a broad survey of a desert community and, regarding association analysis results, similar conclusions were drawn: the divisions at lower levels were much more affected by quadrat size than at the highest level. Subdivisions at the smaller quadrat sizes were usually more meaningful than corresponding ones at larger sizes.

These two reports might suggest that plot size is not necessarily crucial in finding plant assemblage types, since the lower level changes are not significant. However, it is not known *a priori* that plot size would not considerably influence the results. It seems then that the use of various plot sizes is the most desirable sampling strategy for classifications. If the final results suggest that the group structure is stable within a broad range of plot sizes, it may be concluded that the analytical characteristic area (ACA, cf. 3.1.1) is not a fixed size, but an interval and its exact determination is unnecessary. In this case the sites consistently occurring in the same groups can be selected to find a reliable basis for the description of the types. In addition, the quadrats with uncertain group membership give useful information whether the discontinuities in the sample are strong or weak.

If considerable differences occur between classifications based on various plot sizes, the determination of the optimum cannot be avoided. Since there is a good reason to presume that the optima differ with community types, the only theoretically acceptable method would be an iterative strategy. A possible example is as follows:

1. Determine the analytical characteristic area for the whole sample, using the appropriate function f_a.

2. On the basis of the classification of quadrats equal to ACA in size, select n groups as candidates for types.

3. Find the characteristic area, CA, within each class employing function f_c. The analysis ends if

a) ACA = CA for all i, that is the plot size corresponds to all characteristic areas, or

b) ACA = CA for $n - 1$ types, so that a new iteration step is unnecessary. Otherwise go to the next step.

4. Now it may be assumed that the probability of misclassification is the lowest for a group whose characteristic area is best approximated by ACA. The composition of this group is considered final, and all of its quadrats are removed from the sample. Then, the ACA for the remainder is determined. The analysis returns to step 2. if the new ACA differs from the previous one. However, if there is no change in the size of ACA, other groups have to be selected and removed until the new ACA becomes different or all classes are established.

No doubt that many conditions have to be fulfilled in such an analysis, and therefore the above algorithm represents an experiment rather than a practical strategy. The range of plot sizes should be large enough to capture all characteristic areas and the size increment should be small enough to allow for the discrimination between them. Further requirement is the compatibility of functions f_a and f_c. Preferably, these functions should give minimum curves for CA (to ensure within group homogeneity) and a maximum curve for ACA (to facilitate type recognition) in terms of sample heterogeneity. Many techniques suggested to determine characteristic areas do not appear satisfactory for this purpose.

MATTHEWS (1979) substantially contributed to the problem of plot size/classification relationships. Classifications of quadrats based on four different sizes were evaluated by multiple discriminant analysis at four hierarchic levels (2-, 4-, 8- and 16-groups). There was

a good agreement between results using different quadrat sizes at the 2- and 4-cluster levels although the reduction in plot size increased the overlap between the confidence circles of groups. At levels of higher resolution (8- and 16-groups) the tendency to an increase in overlap with decreasing plot size was more marked. In general, the largest plot size gave the clearest and most interpretable result. This study implicitly suggests that at optimum plot size the discrimination among groups is the strongest. By measuring the overall discrimination, however, only an overall optimum is found, but it may be more adequate to measure the degree of overlapping separately for each type. In this way the plot size can be selected at which the given type is most clearly distinguished from the others.

When the objective of clustering is not typification but the elucidation of small-scale pattern, quadrat sampling may prove less useful as demonstrated by WILLIAMS et al. (1969). An agglomerative method, namely a type of information analysis, was applied to a pattern study in a rain-forest vegetation. Data were obtained at three quadrat sizes and with plotless sampling using four different values of neighborhood radius. Classifications of quadrats were hardly interpretable at any size, while the multiple nearest neighbor method produced meaningful results.

The problem of appropriate quadrat size in ordination studies has to be treated separately. At first sight ordinations seem less sensitive to small changes in the data than classifications. Whereas the increase of plot size may result in negligible rearrangements of points in ordination space, the same change may cause the reallocation of sample sites from one group to another. Of course, this statement has to be validated by actual studies.

Ordination of species at different plot sizes was studied by NOY-MEIR and ANDERSON 1971) in a complex manner. Variance-covariance matrices were calculated for each plot size. The matrices were added and then the combined matrix was subjected to principal component analysis (PCA) to obtain an integrated ordination of species. The eigenvalues of the combined matrix were partitioned into contributions from plot sizes. These values were plotted against plot size similarly to pattern analysis. The characteristic area of the community stand was then defined as the plot size where the most striking peak occurred. The method, known as "multiple pattern analysis", was also used by WALKER et al. (1973) and WILLIAMS et al. (1978).

FEKETE and SZŐCS (1974) used a novel approach. The 12 oak-forest species involved in the study were analyzed by PCA using different resemblance coefficients and four plot sizes. Subsequently, the species were classified by sum of squares agglomeration based on the component scores. It was demonstrated that plot size has a remarkable influence on interspecific associations. This effect was most substantial when the correlation coefficient was used.

Species interrelationships were also analyzed by MATTHEWS (1978) who used principal component analysis and multidimensional scaling (MDS) at four plot sizes. The two-dimensional arrangement of species obtained with MDS served as a basis for plexus construction. The ordinations by PCA and MDS were in general agreement, although considerable differences occurred regarding the detailed structure. Results based on the smallest plot size were the most different from the others. GOFF and MITCHELL (1975) compared species ordinations obtained at extremely different levels represented by plot and stand data. The results were fairly similar, although the degree of similarity was influenced by the type of data used.

Some comments were already made on the influence of plot shape, arrangement and sample size in sections 3.1.2–4. This problem is not discussed here again, since no quantitative analyses have been reported on this subject.

4.4.2 The effect of processes in data space

The dependence of ordinations upon the number of species was investigated by AUSTIN and GREIG-SMITH (1968). They found that the less abundant species contributed very little to the ordination of rain-forest stands. It is generally thought that the removal of rare species

has no practical influence on classifications (e.g., species removal prior to association-analysis is a common practice). However, this problem should be exhaustively explored using species ranking followed by successive deletion of less important species.

GOFF (1975) compared species ordinations resulting from different numbers of species. The successive changes of the initial 10-species configuration were differing with the resemblance function used. In the case of the correlation coefficient, the change was most substantial when the next five most common species were included, additional species had relatively smaller influence. By contrast, when COLE's index was used, the addition of the last six species caused the greatest change.

The use of higher taxonomic ranks in phytosociological ordination was proposed by VAN DER MAAREL (1972). He performed principal component analysis on 51 plant communities on the genus, family and order levels. Synecologically interpretable ordinations resulted, but only ordination at the order level was published and discussed. DALE and CLIFFORD (1976) employed divisive information analysis to classify a small set of data at five taxonomic levels. All classifications were similar, but similarity to the species-based classification declined as taxonomic ranks increased. It was recognized that the two highest levels (subfamily, family) were not meaningful. On the contrary, in a large-scale investigation, DEL MORAL and DENTON (1977) found the family-based classification and ordination well-interpretable. In summary it appears that the larger the scale of a given survey the higher are the taxonomic ranks appropriate for analysis.

The influence of data standardization and transformation upon the results has been discussed by several authors (see ORLÓCI 1978a, for review). However, very few studies were devoted to spatial changes whose series may be regarded as spatial processes. In fact, only two papers were found relevant, one by JENSÉN (1978) and another by VAN DER MAAREL (1979b). They both analyzed sets of phytosociological data using different transformations generated by a general exponential function derived by VAN DER MAAREL (1979a, b). Both authors have drawn the same conclusion that intermediate transformations gave always the most "acceptable" results.

4.4.3 The number of clusters

A fundamental question in the cluster analysis of vegetational entities is whether there exists a group structure in the data, and if so, what is the number of distinct groups? This topic will not be discussed here in detail, only a few relevant points will be made. In hierarchical clustering the cut-off level is to be determined below which the subdivision of clusters reflects no real group structure. The process of the analysis may be arrested at a termination point specified by some external criterion (stopping rule) in divisive clustering. However, in the agglomerative or the non-hierarchical methods stopping rules do not apply and the only strategy is the evaluation of a classification process represented by an increase in the number of clusters.

One possibility to test the goodness of classification is offered by discriminant analysis as shown by MATTHEWS (1979). Despite the limitations, i.e., the equality of variance-covariance matrices have to be assumed and the probability level or the dimensionality of the discriminant space are arbitrary, the method is considered robust enough to give useful information about the existence and number of clusters. A simpler alternative applicable to a series of partitions is to examine some ratio of within-group and between-group variances (e.g., RATKOWSKY and LANCE 1978, RATLIFF and PIEPER 1981) or average similarities (POPMA et al. 1983).

4.4.4 The effect of successive algorithmic changes

A classification process generated by successive alterations of the algorithm was explored by LANCE and WILLIAMS (1967) in connection with their flexible strategy. An "*ecological data set*" was classified using six values of β (3.5.1) falling within the interval $[-1, 1]$. Although the authors were unable to define rigorously the value of β, WILLIAMS (1976) in his summary stated that $\beta = -.25$ seems to meet most users' requirements.

The effect of different values for parameters α and β (3.5.3) in parametric mapping was investigated by NOY-MEIR (1974) using several sets of simulated and actual data. He found that $\alpha = 4$ and $\beta = 8$ gave the best results. However, some computational problems occurred when these values were applied to large data sets. Therefore the use of this method for the analysis of realistic data depends on the further improvement of the computer programs

5. Concluding remarks

In Vegetation Science, there are no universally applicable methods of sampling or data analysis. Although the results are not necessarily influenced much by the surveyor's decision in selecting plot characteristics, data type, resemblance function, and multivariate technique, an uncertainty is always present: one cannot predict whether the subjective choices will have significant impact on the conclusions. The present work emphasizes that the problem can be alleviated by studying the processes associated with the different stages of vegetation analysis.

Extending JUHÁSZ-NAGY's (1967, 1976) concept of the dynamism in interspecific associations, a process is defined as a series of changes in real or abstract space encountered by the survey. The different spaces themselves also constitute a series, permitting the distinction of two basic types of processes. Once the primary processes are defined in a given space, the dependent processes are automatically generated in the subsequent spaces. The most frequently used primary processes include changes in plot size and the different data manipulations. The dependent processes are usually represented by a series of classifications, ordinations, resemblance matrices or measurements of a derived variable. Further distinction can be made among primary processes according to the number of controlling parameters simultaneously changed. Accordingly the process is either elementary or complex. It is stressed that complex processes should not be studied until the effect of single controlling parameters is sufficiently known.

In the real space only primary processes can be defined. Most of these are related to one of the four sample plot characteristics; but processes can also be defined in plotless sampling. It was shown that in addition to changes of plot size and shape, sample size, plot spacing and orientation, the non-preferential designs of plot arrangement also constitute a process. The application of processes in real space may help the surveyor to optimize sampling

design, to recognize trends and pattern, and to obtain information about the stability in the results of multivariate analyses.

Manipulations of the data, with the exception of some standardization techniques, can generate primary processes in the data space. The reduction of the dimensionality of data space and the simplification of data type may be used in a pilot study to reduce sampling effort and cost in the main survey. Transformation processes are useful in examining the influence of data type on classifications and ordinations. No sharp distinction can be made between the change of the number of points in data space and the change of sample size.

The primary processes in the space of derived variables and in the resemblance space are of minor importance. In the ordination and classification spaces, processes can be defined if one or more algorithmic parameters need to be specified by the investigator. Non-hierarchical clustering strategies, and some scaling and hierarchical clustering techniques, permit specification of parameters.

It is pointed out that the different spaces are not equally important in the study of dependent processes. However, this fact alone does not account for the unbalanced treatment of the topic in the literature. Most surveys deal with the change of derived variables when affected by sampling, whereas classification and ordination processes received much less attention. One goal of the review embedded in the discussion of dependent processes was to show many unexplored possibilities.

The objective of generating primary processes is to bring about dependent processes that may be informative for various purposes. The diversity of possibilities is most striking in the case of derived variables: the precision and accuracy of statistical estimates, different vegetation parameters and the detection of pattern are all influenced by primary processes in the real space. In fact, Vegetation Science often relies on methods whose principal strategy involves a spatial process in the space of derived variables (pattern analysis, supraindividual diversity studies, etc.).

In the resemblance space, the change of interspecific associations is the most exhaustively examined process. The resemblance of quadrats, especially as affected by sampling, seems just as essential, but much less investigated.

Among the final results of vegetation analysis, the classifications and ordinations are most influenced by the surveyor's decisions. Therefore, in theory, the analysis of ordination and classification processes should constitute the basis of most vegetation surveys. Of course, it would be very expensive and cannot become an everyday practice, but some case studies can be performed to examine some principal questions. However, such a survey is conditioned by the availability of appropriate techniques for the evaluation of results.

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PLANT COMMUNITIES OF CUBA

II. THE RIVERSIDE SCRUB VEGETATION

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Five associations of the tropical evergreen riverside vegetation are described belonging to the Rondeletio-Gesnerietea Borhidi 1979 phytocoenological class. Three of the associations are endemic to Western Cuba, and two for the mountain regions of Oriente. The oriental plant associations are much richer in species, including endemics, than the western ones.

Introduction

In 1979, a systematic survey of the phytocenological units of the vegetation of Cuba was published by BORHIDI, MUÑIZ and DEL-RISCO in this review. The mentioned paper contains the characterization and descriptions of the higher vegetation units listing the names of the studies associations. In this series of papers the ecological structural and phytosociological characteristics of the plant associations are described.

The first part contains the descriptions of the water plant associations of the fresh and salt waters, of the swamp and coastal vegetation. The second part contains the riverside scrub associations, as follows:

Class: **RONDELETIO-GESNERIETEA** Borhidi 1979

Riverside evergreen scrub and suffrutical vegetation, growing on the stony stream-deposits along the montane rivers of the mountain ranges in the Antilles.

Characteristic species and genera: *Rondeletia* spp., *Gesneria humilis* and other spp., *Exostema longiflorum* and other spp., *Buxus* spp., *Eugenia* spp., *Calyptranthes* spp., *Plinia* spp., *Aster* spp., *Ginoria americana* and spp., *Pilea* spp., *Heptanthus* spp. *Sapphoa rigidifolia*, *Phyllanthus* spp., *Erigeron bellioides* and other spp., *Chaptalia* spp., etc.

1. Order: RONDELETIO-GINORIETALIA Borhidi 1979

Riverside evergreen scrubs and suffrutic vegetation growing on different, no serpentine rocks.

Table 1

Rondeletio microphyllae-Gesnerietum humilis Borhidi et Capote

	1	2	3	4	5
Cover %	50	55	60	45	40
Rondeletia microphylla Griseb.*	2.3	2.3	2.2	2.2	1.2
Gesneria humilis L.	2.3	3.3	3.4	2.3	3.3
Erigeron thrincioides Griseb.	+.1	+.1	1.1	—	—
Oldenlandia capillipes Griseb.	+.1	—	—	+.2	—

* Endemic species

1.1 Alliance: ***Rondeletio microphyllae-Ginorion*** Borhidi and Capote 1979

Riverside evergreen scrubs and suffrutescent vegetation in Central and West-Cuba.

Characteristic species: *Rondeletia microphylla*, *R. peduncularis*, *R. pedicellaris*, *R. leonis*, *R. monantha*, *Ginoria americana*, *G. ginorioides*, *Exostema longiflorum*, *Jussiaea decurrens*, *Aster burgessii*, *Cuphaea lobelioides*, *Eugenia oligantha*, *Erigeron thrincioides*, *E. paucilobus*, *E. capillipes*, *Oldenlandia capillipes*, etc.

Associations studied:

1.1.1. **Rondeletio microphyllae-Gesnerietum humilis** Borhidi

Suffrutescent low plant cover on the different (limestone, slate, sandstone) rocks continuously irrigated or flooded by the river stream, formed by

Table 2

Eugenio-Cupheetum lobelioidis Borhidi

	1	2	3	4	5
Cover, %	40	45	50	30	45
Eugenia oligandra Urb.*	1.3	2.3	2.3	+.2	2.3
Cuphea lobelioides Griseb.*	2.3	2.2	2.3	2.2	2.2
Sauvagesia brownei Planch.	+.2	1.2	1.2	—	—
Pilea microphylla (L.) Liebm.	+.2	1.2	+.2	+.2	1.2
Pilea pubescens Liebm.	—	—	+.1	—	—
Anemia wrightii Baker*	—	+.1	—	—	+.1
Erigeron hyoseroides Griseb.	—	—	+.1	—	—

* Endemic species

creeping or decumbent dwarf shrubs in W-Cuba. The association is poor in species, as it can be observed in the Table 1. Type relevé is No. 1 made in the Rio Mantua (Pinar del Rio province), December 1975, by BORHIDI and R. CAPOTE.

1.1.2. **Eugenio-Cuphaeetum lobelioidis** Borhidi

Suffrutescent riverside association mainly on limestone rocks, in the Sierra de los Organos. Five representative relevés were made by BORHIDI in 1975–1976, near to Sumidero and Guane. Type relevé No. 3 (Table 2) at the Resolladero of the Cuyaguateje river.

1.1.3. **Exostemo-Ginorietum americanae** Borhidi and Capote

Riverside evergreen scrub association with two layers growing on limestone rocks of the Sierra del Rosario and perhaps in other limestone mountains as well. Five representative relevés were made by BORHIDI and R. CAPOTE in different river valleys of the Sierra del Rosario near to Soroa, San Diego de los Baños and Rangel in 1975 and 76. Type relevé No. 1 (Table 3) made in Valley of Rio San Diego, November 1975.

2. Order: RONDELETIO-PURDIAEETALIA Borhidi 1979

Riverside scrub vegetation on humid serpentine rocks of the mountains of Oriente (East Cuba).

Characteristic species: *Rondeletia pachyphylla*, *R. alaternoides*, *Purdiaea* spp., *Leucocroton* spp., *Heptanthus* spp., *Pilea* spp., *Mozartia* spp., *Myrcia* spp., *Calyptranthes* spp., *Gundlachia* spp., *Schmidtottia* spp., *Chaptalia* spp., etc.

Table 3

Exostemo-Ginorietum americanae Borhidi et Capote

	1	2	3	4	5
Shrub layer, 1 m high, cover %	50	60	60	55	45
Ginoria americana Jacq.	3.4	4.4	4.5	3.4	3.3
Mithranthes ottonis Berg	+.1	1.1	+.1	1.2	1.2
Herb layer, 30 cm high, cover %	70	65	70	80	95
Rondeletia microphylla Griseb.*	2.3	2.2	2.3	3.3	3.3
Exostema longiflorum (Lamb.) R. et S.	1.2	1.1	—	1.2	+.2
Gesneria humilis L.	3.3	2.3	2.3	3.4	4.4
Jussiaea decurrens (Walt.) Dc.	+.1	—	—	+.1	—
Aster burgessii Britt.*	—	—	+.2	—	+.1

* Endemic species

Fig. 1. A representative stand of the association *Exostemo-Ginorietum americanae* Borhidi and Capote in the valley of Rio Palacios, Pinar del Rio Province, West-Cuba. (Photo: A. BORHIDI)

Fig. 2. Exostema longiflorum (Lamb.) Roem. et Schult., a characteristic species of the *Exostemo-Ginorietum americanae* association. (Photo: A. BORHIDI)

2.1. Allience: ***Purdiaeo-Rondeletion pachyphyllae*** Borhidi 1979

Riverside sclerophyllous evergreen scrub vegetation in the serpentine mountains of the Northern part of Oriente, represented by a number of different associations composed by vicariant species of the same genera.

Characteristic species: *Rondeletia pachyphylla*, *R. shaferi*, *R. alaternoides*, *R. vacciniifolia*, *Calyptranthes monocarpa*, *C. moaensis*, *C. toaensis*, *C. pseudomoaensis*, *Leucocroton stenophyllus*, *L. acunae*, *L. obovatus*, *Purdiaea shaferi*, *P. ekmanii*, *P. moaensis*, *P. velutina*, *Acrosynanthus revolutus*, *Oldenlandia polyphylla*, *Schmidtottia cubensis*, *S. monantha*, *S. uliginosa*, *Buxus foliosa*, *Exostema stenophyllum*, *Heptanthus cordifolius*, *H. shaferi*, *Chaptalia nipensis*, *C. shaferi*, *Phyllanthus chamaecristoides*, etc.

Associations studied:

2.1.1. **Exostemo-Leucocrotonetum stenophylli** Borhidi

The riverside serpentine scrub-association of the Sierra de Nipe, formed by a dense shrub and a low dispersed herb layer, many lianes and few epiphytes. Five representative relevés were made by Borhidi February 1976 in the valley of Rio Guaro Rio Sojo, and Rio Piloto, in the Sierra de Nipe. Type relevé: No. 1 (Table 4) made in the Rio Guaro above the waterfall.

2.1.2. **Buxo foliosae-Acrosynanthetum revoluti** Borhidi and Muñiz

The riverside serpentine scrub association in the montane rivers of the Moa range. Structure of the community is similar to that of the former association, but lianes are poorly represented. High participation of endemics is an

Fig. 3. A representative stand of the riverside scrub association *Exostemo-Leucocrotonetum stenophylli* Borhidi, in the valley of the Rio Guaro, Nipe Mountains, Holguin Province (Oriente). (Photo: A. Borhidi)

Table 4

Exostemo-Leucocrotonetum stenophylli Borhidi

	1	2	3	4	5
Shrub layer, height: 1–2 m, cover %	60	50	65	70	55
Leucocroton stenophyllus Urb.*	2.3	2.2	2.3	3.3	2.2
Rondeletia pachyphylla Krug et Urb.*	2.2	2.2	2.2	1.1	+.1
Calyptranthes monocarpa Urb.*	—	—	—	+.2	+.1
Schmidtottia cubensis (Standl.) Urb.*	—	—	—	1.1	1.1
Scolosanthus reticulatus Borhidi*	+.1	1.1	—	—	—
Psychotria linearifolia Urb.*	—	—	+.1	—	—
Brya hirsuta Borhidi*	—	—	—	1.1	+.1
Calycogonium rosmarinifolium Griseb.*	1.1	+.1	+.1	+.1	—
Ateramnus recurvus (Urb.) Rothm.*	+.1	+.1	—	1.2	+.1
Gundlachia apiculata Britt. et Blake*	—	+.2	—	—	—
Purdiaea nipensis M. Vict.*	+.1	+.1	+.1	—	+.1
Clidemia rubrinervis Cogn.	+.1	—	—	+.1	—
Cassia shaferi Britt. et Wils*	—	+.1	—	—	—
Hypericum fasciculatum Lam.	+.2	1.2	1.2	—	+.2
Phyllanthus shaferi Urb.*	+.2	—	+.1	+.1	—
Herb layer, height: 5–40 cm, cover %	20	25	15	15	25
Exostema stenophyllum Britt.*	1.1	1.2	+.2	+.2	1.1
Spaniopappus shaferi (Robins) King et Robins.*	+.1	+.r	—	—	—
Heptanthus cordifolius Britt. et Wils.*	+.2	+.2	+.2	—	—
Chaptalia nipensis Urb.*	+.r	+.1	—	+.1	+.r
Salvia cubensis Britt.*	—	+.1	—	+.1	+.1
Paepalanthus pungens Griseb.*	1.2	2.2	1.2	1.2	2.2
Lianes					
Platygyne triandra Borhidi*	+.1	+.1	+.1	—	—
Serjania nipensis Urb.*	—	—	+.1	+.1	+.1
Harnackia bisecta Urb.*	—	—	—	+.1	+.r
Rajania linearis Howard*	—	+.1	+.r	—	—
Epifites					
Oncidium ghibertianum A. Rich.	—	—	—	+.1	—

* Endemic species

outstanding feature. Five relevés were made by BORHIDI and MUÑIZ March 1970 in the valley of the Rio Iberia about 550–600 m a.s.l. Type relevé is the No. 1 (Table 5).

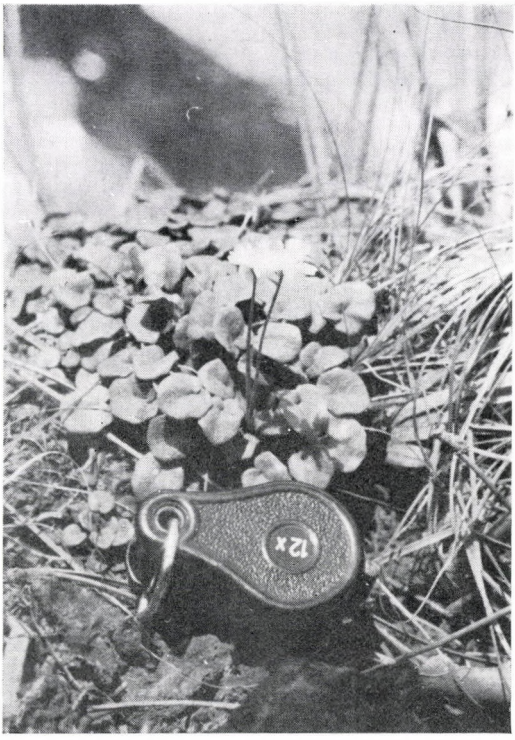

Fig. 4. Heptanthus cochlearifolius Britt. a characteristic endemic species of the *Exostemo-Leucocrotonetum stenophylli* Borhidi. (Photo: A. BORHIDI)

Fig. 5. Paepalanthus riparius Mold., a characteristic endemic species of the association *Buxo foliosae-Acrosynanthetum revoluti* Borhidi in the valley of Rio Iberia, Cuchillas de Moa. (Photo: A. BORHIDI)

Table 5

Buxo foliosae-Acrosynanthetum revoluti Borhidi et Muñiz

	1	2	3	4	5
Shrub layer, height: 1–2 m, cover %	60	70	75	80	70
Buxus foliosa (Britt.) Urb.*	2.3	3.3	3.4	2.3	1.2
Acrosynanthus revolutus Urb.*	3.3	2.2	2.2	3.4	2.3
Rondeletia pachyphylla Kr. et Urb.*	1.2	1.2	1.2	2.2	2.3
Calyptranthes pseudomoaensis Borhidi et Muñiz*	—	+.2	+.2	—	—
Schmidtottia monantha Urb.*	+.1	—	—	+.1	—
Purdiaea velutina Britt. et Wils.*	1.1	1.2	—	1.1	1.2
P. moaensis M. Vict.*	+.2	+.1	1.2	+.1	+.2
Moacroton ekmanii (Urb.) Croiz.*	—	—	+.1	+.r	—
Psychotria moaensis Britt. et Wils.*	+.1	+.1	—	—	+.1
Ateramnus recurvus (Urb.) Rothm.*	+.1	+.2	+.2	1.2	+.1
Miconia moaensis Alain*	+.1	—	—	+.1	—
Ossaea baracoensis Borhidi et Muñiz*	—	—	+.1	—	+.1
Hypericum fasciculatum Lam.*	+.1	+.2	1.2	1.2	1.2
Scolosanthus lucidus Britt.*	+.2	+.2	—	—	+.2
Croton monogynus Urb.*	+.1	—	—	—	+.r
Rondeletia vaccinifolia Urb.*	—	—	—	1.2	+.r
Pithecellobium nipense Britt. et Wils.*	—	—	1.1	—	—
Garcinia polyneura (Urb.) Borhidi*	—	+.1	+.2	—	—
Herb layer, height: 5–40 cm, cover %	30	35	20	15	40
Paepalanthus riparius Mold.*	2.3	2.3	2.2	1.2	2.3
Heptanthus shaferi Britt.*	+.2	+.1	—	+.1	—
Chaptalia shaferi Britt.*	+.1	+.r	+.r	+.r	+.1
Oldenlandia polyphylla Urb.*	—	+.1	—	+.1	—
Mniochloa pulchella (Griseb.) Chase*	—	—	—	+.2	—
Pilea fruticulosa Morton*	+.2	—	+.1	+.2	2.2
Phyllanthus erythrinus Muell. Arg.*	1.1	—	—	—	1.2
Lianes					
Mikania alba Taylor	—	+.1	+.1	—	—
Epiphytes					
Octadesmia oligophylla Schltr.	—	—	+.1	—	—
Pinguicula lignicola Barnh.*	—	+.r	—	—	—

* Endemic species

2.2. Alliance: ***Gundlachio-Bryon subinermis*** Borhidi 1979

Riverside scrubs pioneering in the sandbanks deposited by the lower part of the river streams of the mountain rivers in Oriente.

Characteristic species: *Gundlachia lindeniana*, *G. cubana*, *G. apiculata*, *Brya subinermis*, *B. chrysogonii*, *Tabebuia rivularis*, *Ginoria montana*, *G. arborea*, etc.

Association studied:

2.2.1. **Gundlachio-Bryetum subinermis** Borhidi and Muñiz

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REPRODUCTIVE ALLOCATION IN THE STAGES OF SANDY SUCCESSION II.

ERIGERON CANADENSIS L. AND *POLYGONUM ARENARIUM* W. ET K.*

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Reproductive allocation (RA) of two annual species (*Erigeron canadensis*** and *Polygonum arenarium*) was studied in two stages of sandy primary succession in an annual grassland and in a *Festucetum vaginatae danubiale*. The sample plants were separated into fertile parts, seeds, assimilating parts and roots. The weight of other species living in the sample sites was determined. The factors influencing the variability of RA were examined by path analysis. In both species the direct influence of the assimilating organs on the fertile part is strong and positive, that of the root is small or negative, while the cenological direct effect is not significant. Although the direct influence of the cenological components of the two different communities (the annual and perennial grasslands) on RA cannot be shown by path-analysis, it has become obvious that the cenological variables included strongly influence the variability of the weight of vegetative parts of the two species investigated, i.e. their influence on RA is indirect.

Introduction

Despite the relatively short past of research on reproductive allocation, a number of various theories and results have been published whose knowledge necessitates further experiments to draw new conclusions.

Knowledge of the plasticity of allocation is indispensable for understanding succession. When studying reproductive strategies, the analysis of the following problems is of fundamental importance:

1. What proportion of the biomass is allocated to reproduction by plants?
2. How constant is this proportion and to what extent is the environment modifying?
3. How efficient is the reproduction considering the allocated biomass and energy?

In our previous paper (FEKETE and MELKÓ 1981) we attempted to picture the various theories and results. It is mentioned in advance that the results published here support the above considerations.

GROSS and SOULE (1981) studied the biomass allocation of male and female individuals, and the proportion of sexes in a *Silene alba* population. Growth characteristics of this species in three seed size categories were also examined. It was found that seed size considerably influenced the size of mature plants and the flower production of both males and females, but had no influence on the proportion of sexes. Male and female plants differed in the proportion of total biomass allocated to vegetative and reproductive structures, and these differences were consistent throughout all seed size categories. The reproductive allocation of female plants was larger, which is a possible cause of the relatively large size of mature females.

* Tece studies No. 29.

** *Erigeron canadensis* L. 1753 = *Conyza canadensis* (L.) Cronquist 1943.

STEWART and THOMPSON (1982) studied the allocation to vegetative and reproductive structures in six perennial species in three different places (quarry, grassland, scrub). There was only a slight difference among the three stages at *Carex flacca* and *Centaurea nigra*, but a marked difference was indicated at the other four species, *Leontodon hispidus*, *Plantago lanceolata*, *P. media* and *Poterium sanguisorba*. Population reproductive effort (RE) was highe in the quarry and lower in the grassland. They attributed the differences among habitats to the different intensity of competition. On their opinion the RE of individuals may considerably differ from the population RE, and the process of succession is not always parallel to tendencies in RE reduction: stands at late stages may include populations with RE larger than that of a population from an intermedier stage.

WAITE and HUTCHINGS (1982) studied the plasticity of energy allocation in *Plantago coronopus*. Under greenhouse circumstances the plants behaved just like annuals. Energy allocation was slightly influenced by nutrients and considerably by closeness; RA considerably decreased as closeness increased. There were considerable differences among the three populations in the energy allocation samples, their strategies changed according to the differences in habitats.

GRACE and WETZEL (1981) carried out experiments on *Typha latifolia* coming from three places of different successional maturity in order to separate genotypic and phenotypic variation in biomass allocation. According to their results the open marsh population is mainly nutrient-limited, while the woods marsh population is light-limited. The cattail marsh population was transitional between the two others. The sexual and vegetative reproduction required a larger biomass allocation in the open marsh population than in the other two populations. Under uniform circumstances in gardens the differences in the allocation of biomass were preserved. A biotype transplantation showed that under nutrient-limiting conditions the habitat of woods and cattail marsh populations is more productive than that of the open marsh population. Under light-limiting conditions, however, there were no differences in productivity among biotypes, i.e. genotypic and phenotypic variation in the biomass allocation, contributed to the growth and reproduction in the localities of different successional maturity.

According to JAKSIĆ and MONTENEGRO (1979), annuals give responses differing from those of perennials under unchanged experimental circumstances. However, a similar examination of perennials would be even more complicated, as vegetative RA has to be also considered.

The aim of the present study, similarly to a previous survey (FEKETE and MELKÓ 1981), is to obtain a picture of the biomass allocation in the annuals investigated during succession. The main problems are: What proportion of the biomass is allocated to reproduction? How constant is this proportion? How much is it modified by environment partly through the "inner effects" (within individuals) and partly by the components of the community (interspecific effect).

In our previous paper we tried to interpret the modifying effect of the environment, i.e. the effect of closure. It was shown that the value of relative reproductive allocation of the investigated species (*Festuca vaginata*, *Alyssum montanum* ssp. *gmelini*, *Arenaria serpyllifolia*, *Silene conica*) is significantly different in the various successional stages. The scheme applied made it also possible to measure the influence of the inner components (those within plants) and the external (cenological) ones on RA. (The path analysis technique used here is described by LI 1955, LEROY 1960 and SVÁB 1973. For the interpretation of the inner and external components and effects, see Fig. 1.) In the annuals the direct influence of the assimilating organ was significant at every stage, that of the root-weight was less significant. The effect of the other species was also small. The RA of annual species is different in the successional stages. In closed stages not only the effect of assimilating weight but the cenological direct influence was also significant in *Festuca vaginata*.

Regarding methodologies and objectives the present survey is a continuation of the work cited above. Emphasis is on the fairly flexible annual life form. At the same time it is an improved version of the preceding work, because the studies on crop weight are extended to measuring seed production.

Material and method

The study area was on the sand dunes near Fülöpháza in the Kiskunság National Park (Great Hungarian Plain), in an annual open sandy grassland *(Brometum tectorum)* and in a semi-closed, perennial one (*Festucetum vaginatae danubiale*).

The annual grassland is constituted by the following species: *Erigeron canadensis*, *Polygonum arenarium*, *Secale silvestre*, *Kochia laniflora*, *Tragus racemosus*, *Medicago minima*, *Bromus squarrosus*, and *Cenchrus pauciflorus*. The species mentioned below live in the *Festucetum vaginatae danubiale* community: *Festuca vaginata*, *Stipa sabulosa*, *S. capillata*, *Koeleria glauca*, *Cynodon dactylon*, *Silene conica*, *Carex liparicarpos*, and *Scabiosa ochroleuca*. Two annual species, *Erigeron canadensis* L. and *Polygonum arenarium* W. et K. were included in the study. Data were collected in both communities.

Erigeron canadensis L.

Annual plant, reproduces only by seeds, germinates in autumn and survives winter. Flowering time from June to November. Seeds germinate from early spring to late autumn if the humidity required is available. If the upper soil layer becomes dry, the young plants die early. In the summer it can grow in dry places only in the shelter of other plants. Prefers loose sandy soils, on which it may constitute stands containing no other species. In some places it has already been incorporated in the natural sandy successional sere as well.

Polygonum arenarium W. et K.

Annual plant, reproduces only by seeds. Found in large numbers in loose, poor sandy grasslands. It is not of weed character. It is blooming from June to September.

Both species are found mainly in open annual sandy grasslands. In closed swards *Erigeron canadensis* is present only sporadically. *Polygonum arenarium* occurs in semiclosed perennial sandy grasslands as well.

Only fertile plants were used in this study. The plants were collected from sample plots of different size. The size of plots was chosen after an estimation of the area of interaction between the plants investigated and the individuals of other species. For *Erigeron canadensis* circular plots with diameter of 30 cm were considered optimal in both *Festucetum vaginatae danubiale* and the annual grassland. For sampling *Polygonum arenarium* a smaller area was necessary, plots with diameter of 20 cm were taken in *Festucetum vaginatae*, while the diameter was 15 cm in the annual sward. All plant material was collected from the plots. After clearing the plant samples, each individual of the two species examined was split into fertile part (including seeds), assimilating parts and root.

The other species in the plots were also collected, cleaned and grouped as follows. In case of both species sampled great importance was attached to the conspecific individuals and to *Festuca vaginata* in the perennial grassland. The conspecific individuals and *Festuca vaginata* were treated as separate groups in the analyses while the group of "the other species" was formed to contain the species of smaller abundance in the sample plot. The purpose of forming these different groups was to examine the direct and indirect influences of cenological components.

Assuming that annuals mutually influence one another, they are considered equal in importance. However, the interaction between perennials and annuals is supposingly unidirectional such that only perennials influence annuals.

The separated plant parts, as well as the plants grouped according to the above considerations were exiccated at a temperature of 110 °C, and then weighed.

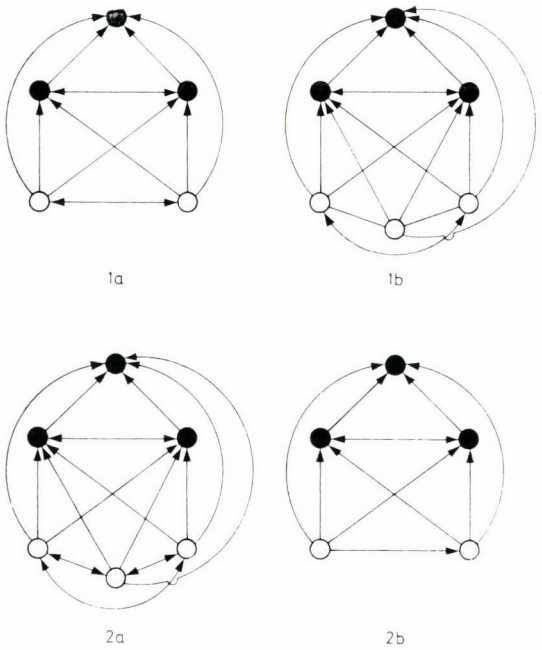
The factors influencing the variability of RA were analyzed by path analysis (FEKETE and MELKÓ 1981).

Results and discussion

It is seen in Table 1 that considering any part of *Erigeron canadensis*, the weight of samples taken from the annual sward is the multiple (almost tenfold) of those from the perennial grassland but the correlation between these parts is almost the same in both sample sites (Table 2).

In the weight of each separated part of *Polygonum arenarium*, the difference between habitats is smaller. The correlations, however, are not the same, being lower in the perennial grassland than in the annual grassland (Tables 1 and 2).

In the analyses, the weight of fruit, seed, assimilating part, root and that of cenological components were considered as variables. The correlations between these variables are summarized in Table 2. These values represent the starting point for path analysis. The possible path schemes are shown in Fig. 1, illustrating the relationship between the individual and cenological levels and also the way of interaction between the variables. The construction of path schemes was based on our previous study (FEKETE and MELKÓ 1981).



Figs 1—2. The four types of path schemes applied: *1a. Erigeron canadensis* in open annual sward. *1b. Erigeron canadensis* in semi-closed perennial sward. *2a. Polygonum arenarium* in open annual sward. *2b. Polygonum arenarium* in semi-closed perennial sward. Full circles: variables of the individual level (on the top: reproductive weight; the lower two: weight of assimilating organs, root weight). Open circles: variables on the supraindividual (cenological) level

Table 1

Average weights (in grammes)

	Weight of crops	Weight of assimilation organs	Root weight	Weight of seeds	Weight of *Erigeron*	Weight of *Polygonum*	Weight of *Festuca*	Weight of other species
Erigeron								
in *Brometum*	0.35	0.45	0.10	0.21	4.42	—	—	0.49
in *Festucetum*	0.04	0.07	0.02	0.02	0.21	—	9.70	1.77
Polygonum								
in *Brometum*	0.05	0.13	0.02	0.03	1.02	0.70	—	0.16
in *Festucetum*	0.01	0.02	0.01	0.01	—	—	3.69	5.77

Table 2

Coefficients of correlation

	I *Erigeron* in *Brometum*	II *Erigeron* in *Festucetum*	III *Polygonum* in *Brometum*	IV *Polygonum* in *Festucetum*
r_{12}	0.8839	0.8903	0.9133	0.7580
r_{13}	0.6016	0.7509	0.8735	0.5568
r_{15}	−0.0606	0.0994	0.2758	−0.1038
r_{16}	−0.0620	−0.0770	−0.1565	−0.5228
r_{17}	—	0.1728	0.0548	—
r_{42}	0.8924	0.7757	0.9326	0.7747
r_{43}	0.7462	0.8506	0.9003	0.7207
r_{45}	−0.1848	0.0027	0.3042	−0.2912
r_{46}	0.1808	−0.1709	−0.2916	−0.4600
r_{47}	—	0.2218	0.1047	—
r_{23}	0.8595	0.7771	0.9635	0.5646
r_{25}	0.1461	0.1830	0.5319	−0.2029
r_{26}	0.2469	−0.0592	−0.0656	−0.6189
r_{27}	—	−0.1127	−0.0773	—
r_{35}	0.1149	0.0202	0.4629	−0.1062
r_{36}	0.5092	−0.1353	−0.0416	−0.1662
r_{37}	—	−0.0814	−0.1698	—
r_{56}	−0.0732	−0.3091	0.3698	0.2891
r_{57}	—	0.3123	−0.0832	—
r_{67}	—	−0.1167	−0.3601	—

I–IV. I. 1. Crop. 2. Weight of assimilation organs. 3. Root weight. 4. Weight of seeds. 5. Weight of *Erigeron* individuals. 6. Weight of other species. II. 5. Weight of *Festuca* individuals. 6. Weight of *Erigeron* individuals. 7. Weight of other species. III. 5. Weight of *Polygonum* individuals. 6. Weight of *Erigeron* individuals. 7. Weight of other species. IV. 5. Weight of *Festuca* individuals. 7. Weight of other species

Erigeron canadensis

In the annual sward, the inner effect of this species, i.e. the effect of the assimilating part on the fertile part is large (Table 3), that of the root is also large but negative. In *Festucetum vaginatae*, however, the opposite character of the two organs disappears as the effect of root becomes positive, but both effects are weakened (Table 3).

Examinations related to the seeds. In the annual sward, the assimilating parts have a weaker influence on seeds than on the fruit (Table 4). The negative effect of the roots considerably decreases. In the perennial sward, however, the nature of the inner effect changes: the effect of the assimilating organs is considerably weakened, while that of the root increases to a great extent in a positive direction.

Cenological effect: considering either the fruit (Table 3) or the seed (Table 4), no significant effect of the cenological components can be observed in the annual and the perennial sward. The conspecific individuals do not influence directly the fertile part, either.

However, if the vegetative parts of the plant are considered it is found that there is a direct influence at community level in the annual sward. Intraspecific competition has a fairly strong negative effect on the assimilating

Table 3

Direct (individual and cenological) effects on crop and direct (cenological) effects on assimilating organs and root of Erigeron canadensis and breaking down of the multiple determination coefficient (R^2) in open annual and semi-closed perennial sward. For explanation of indices see Table 2

Annual sward (*Brometum tectorum*)		%	Semi-closed perennial sward (*Festucetum vaginatae danubiale*)		%
$p_{21} = 1.4041$	$p^2_{21} = 1.9715$	197.15	$p_{21} = 0.7745$	$p^2_{21} = 0.5999$	59.99
$p_{31} = -0.6052$	$p^2_{31} = 0.3663$	36.63	$p_{31} = 0.1491$	$p^2_{31} = 0.0222$	2.22
$p_{51} = -0.2047$	$p^2_{51} = 0.0419$	4.19	$p_{51} = -0.0071$	$p^2_{51} = 0.0001$	0.01
$p_{61} = -0.1155$	$p^2_{61} = 0.0133$	1.33	$p_{61} = 0.0191$	$p^2_{61} = 0.0004$	0.04
			$p_{71} = 0.2767$	$p^2_{71} = 0.0766$	7.66
common $(2p_ip_jr_{ij}) = -1.5286$			common $(2p_ip_jr_{ij}) = 0.2275$		
total $R^2 = 0.8644$			total $R^2 = 0.8042$		
$p_e = 0.3682$	$p^2_e = 0.1356$		$p_e = 0.4425$	$p^2_e = 0.1958$	
$p_{52} = -0.5390$			$p_{52} = -0.3159$		
$p_{62} = -1.2016$			$p_{62} = -0.2030$		
$p_{53} = 0.6948$			$p_{72} = 0.3082$		
$p_{63} = 1.5928$			$p_{53} = 0.4374$		
			$p_{63} = 0.1057$		
			$p_{73} = -0.4451$		

parts, and a strong positive effect on the roots. The other annual species have a similar, but an even more increased effect (Table 3).

In the perennial sward the effect of *Festuca* and the other species on the assimilating organs and the root of *Erigeron* is intermediate.

Table 4

Direct (individual and cenological) effects on the seeds of Erigeron canadensis and breaking down of the multiple determination coefficient (R^2) in open annual and semi-closed perennial sward For explanation of indices see Table 2

Annual sward (*Brometum teetorum*)		%	Semi-closed perennial sward (*Festucetum vaginatae danubiale*)		%
$p_{24} = 0.9609$	$p_{24}^2 = 0.9233$	92.33	$p_{24} = 0.2896$	$p_{24}^2 = 0.0839$	8.39
$p_{34} = -0.0797$	$p_{34}^2 = 0.0064$	0.64	$p_{34} = 0.6256$	$p_{34}^2 = 0.3914$	39.14
$p_{54} = -0.3189$	$p_{54}^2 = 0.1017$	10.17	$p_{54} = -0.0404$	$p_{54}^2 = 0.0016$	0.16
$p_{64} = -0.0392$	$p_{64}^2 = 0.0015$	0.15	$p_{64} = -0.0451$	$p_{64}^2 = 0.0020$	0.20
			$p_{74} = 0.3127$	$p_{74}^2 = 0.0978$	9.78
common $(2p_ip_jr_{ij}) = -0.2325$			common $(2p_ip_jr_{ij}) = 0.2275$		22.75
total, $R^2 = 0.7066$			total, $R^2 = 0.8042$		80.42
$p_e = 0.5417$	$p_e^2 = 0.2934$		$p_e = 0.4425$	$p_e^2 = 0.1958$	

For path value on assimilation organs and root of cenological components see Table 3.

Polygonum arenarium

The direct effect of the assimilating mass on RA, both on the crop and the seed, is large, while the other direct influences cannot be taken into consideration (Tables 5 and 6). In the annual sward the assimilating mass has a strong influence on the fruits, and a slightly decreased effect on seeds. The root has a very small and negative effect on the crop, and almost no influence on seeds. In the perennial sward the effect of the assimilating organs on the crop is slightly smaller and the root plays a bit more important role (Table 5).

In the annual sward the cenological components have no direct effect on crop and seed (Tables 5 and 6), but considerably influence the assimilating mass. The intraspecific control affecting the assimilating mass is very strong, it is intermediate in case of the root and negative in case of the sward. *Erigeron* has no remarkable direct and indirect effects on the assimilating mass and root of *Polygonum*. The role of the other species is significant, having a strong opposite effect on assimilating mass and root (Table 5).

Festuca vaginata has practically no influence on crop, seed, assimilating mass and root. The other species (annuals and perennials), in the perennial sward however, have a strong direct influence on assimilating mass and a weak influence on root (Table 5).

Table 5

Direct (individual and cenological) effects on crop and direct (cenological) effects on assimilating organs and root of Polygonum arenarium and breaking down of the multiple determination coefficient (R^2) in open annual and semi-closed perennial sward. For explanation of indices see Table 2

Annual sward (*Brometum tectorum*)			%	Semi-closed perennial sward (*Festucetum vaginatae danubiale*)			%
$p_{21} =$	1.0002	$p^2_{21} =$ 1.0004	100.04	$p_{21} =$	0.6512	$p^2_{21} =$ 0.4241	42.41
$p_{31} =$	−0.0902	$p^2_{31} =$ 0.0081	0.81	$p_{31} =$	0.1891	$p^2_{31} =$ 0.0358	3.58
$p_{51} =$	−0.2054	$p^2_{51} =$ 0.0422	4.22	$p_{51} =$	0.0758	$p^2_{51} =$ 0.0057	0.57
$p_{61} =$	−0.0152	$p^2_{61} =$ 0.0002	0.02	$p_{61} =$	−0.0948	$p^2_{61} =$ 0.0090	0.90
$p_{71} =$	0.0416	$p^2_{71} =$ 0.0017					
common $(2p_ip_jr_{ij}) =$		−0.3742		common $(2p_ip_jr_{ij}) =$		0.2487	
total, $R^2 =$		0.6785		total, $R^2 =$		0.7233	
$p_e =$	0.5670	$p^2_e =$ 0.3215		$p_e =$	0.5260	$p^2_e =$ 0.2767	
$p_{52} =$	0.8871			$p_{52} =$	0.0130		
$p_{62} =$	−0.2914			$p_{62} =$	−0.7708		
$p_{72} =$	0.6601			$p_{53} =$	−0.0655		
$p_{53} =$	−0.5101			$p_{63} =$	0.2690		
$p_{63} =$	0.1406						
$p_{73} =$	−0.7976						

Table 6

Direct (individual and cenological) effects on the seeds of Polygonum arenarium and breaking down of the multiple determination coefficient (R^2) in open annual and semi-closed perennial sward. For explanation of indices see Table 2

Annual sward (*Brometum teetorum*)			%	Semi-closed perennial sward (*Festucetum vaginatae danubiale*)			%
$p_{24} =$	0.9092	$p^2_{24} =$ 0.8266	82.66	$p_{24} =$	0.5399	$p^2_{24} =$ 0.2915	29.15
$p_{34} =$	0.0243	$p^2_{34} =$ 0.0006	0.06	$p_{34} =$	0.4159	$p^2_{34} =$ 0.1730	17.30
$p_{54} =$	−0.0908	$p^2_{54} =$ 0.0082	0.82	$p_{54} =$	−0.1211	$p^2_{54} =$ 0.0147	1.47
$p_{64} =$	−0.1547	$p^2_{64} =$ 0.0239	2.39	$p_{64} =$	−0.0567	$p^2_{64} =$ 0.0032	0.32
$p_{74} =$	0.1185	$p^2_{74} =$ 0.0140	1.40				
common $(2p_ip_jr_{ij}) =$		−0.0207		common $(2p_ip_jr_{ij}) =$		0.3405	
total, $R^2 =$		0.8628		total, $R^2 =$		0.8228	
$p_e =$	0.3837	$p^2_e =$ 0.1472		$p_e =$	0.4210	$p^2_e =$ 0.1772	

For path value on assimilation organs and root of cenological components see Table 5.

The cenological effect on seeds is insignificant in the annual and perennial swards. Summarizing the results it can be stated that, although the effect of cenological components in two types of swards (annual and perennial) on the RA of the two species investigated cannot be revealed by path analysis, the two different habitats have different physiological effect on plants. This is reflected by not only the differences in direct and indirect effects of the vegetative plant parts on RA, but also by the different weight of plants taken from the two contrasted sward types according to successional stages.

The analysis showed that cenological components indirectly influence RA and control the allocation of the biomass of the vegetative structure.

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SECONDARY SUCCESSION IN A HERBACEOUS VEGETATION AFTER DEFORESTATION*

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The succession in a herbaceous vegetation developed on a site formerly occupied by sessile oak-turkey oak forest (*Quercetum petraeae-cerris*) is described and discussed. Prior to the deforestation in the fall of 1979, the floristic composition and the cover of each species in the understory had been determined. After deforestation, three transects, each consisting of five permanent quadrats, were established, transect 1 on the edge of the former forested area adjacent to a secondary grassland community, transects 2 and 3 within the former forest.

The vegetational change in the permanent quadrats within the deforested area was different from that observed at the edge. As early as the next year after cutting, the number of species in the internal part of the study area was more than the double of that determied in the forest. Later, this increase was slowed down. In the quadrats at the edge there were always numerous species present during the study.

After three years the plant cover on the deforested area was 6.4 times higher than the cover of herbs in the forest. Species with high cover values include five species dominant in the forest community, four species with relatively small cover in the forest, and seven newly established and quickly spreading species.

In the third year of the secondary succession the average plant cover in transect 1 was only a little higher than the cover in the other two.

Dominance/diversity curves indicate that there was no species in the transects with extremely high cover. Almost equally high dominance of three or four species is characteristic especially of transect 1, and also of transect 3. For this reason, the curves almost fit a straight line. The curves based on the data of transect 3 are of sigmoid shape.

By the third year the diversity values in the transects have got close to one another, with the most significant changes occurring in transect 3.

In transects 2 and 3, high disorder was observed after cutting. The disorder, however, decreased by 1982.

The life form of 91% of the species in the understory was hemicryptophyte, geophyte and biennial. The proportion of these categories decreased during the three years of study, while the number of therophytes increased. Plant strategies changed according to the changes in life forms.

The life form diversity was higher in transect 1 than in the transects from within the study area.

The proportion of diploid and polyploid species increased over the years in all the three transects with the exception of transect 1 in 1981. The proportion of diploids and polyploids was the largest in transect 3 throughout the study.

Introduction

The compositional and functional characteristics of the vegetation at a given site are determined in part by ecological factors. Any ecological change may result in changes in the vegetation. Recently, the environment of natural communities is many times changed by the

* "Síkfőkút Project" No. 82.

economic activity of man. More and more reports have been published on regeneration and degradation processes induced by the new environmental conditions. The secondary succession after fire and the abandonment of agricultural lands and construction sites is discussed by ODUM (1960), SHAFI and YARRANTON (1973), NICHOLSON and MONK (1974), BAZZAZ (1975), RILEY (1975), DENSLOW (1980), UHL et al. (1981) and ZWETSLOOT (1981), among others. There are relatively few papers dealing with succession after cutting temperate forests (JUHÁSZ-NAGY 1979, PAPP and PRÉCSÉNYI 1980). JUHÁSZ-NAGY analyzed the succession in a degraded oak forest and a honeylocust stand after deforestation. He made a distinction between "exterior" and "interior" degradation.

GRIME (1979) distinguishes between two types of secondary succession as affected by "productive" and "non-productive" environment. The prevailing plant strategies in an environment with climate and soil promoting the development of highly productive forest communities are different from those in a non-productive environment in which succession follows other strategies to reach climax.

Besides the study of plant strategies the estimation of diversity changes also yields valuable information about succession processes. The various forms of diversity are related to the maturity, organization and stability of communities and their resistence against perturbations, etc. (MCNAUGHTON 1968, MARGALEF 1968).

The present paper describes the floristical and structural changes at the early stages of a secondary succession in the herbaceous vegetation remained after cutting down a sessile oak-turkey oak forest.

Description of the study area

The study area lies approximately 6 kilometres east of the "Síkfőkút Project" research station, northeast of Eger, in the foothills of the northern Hungarian Range (Fig. 1). It is

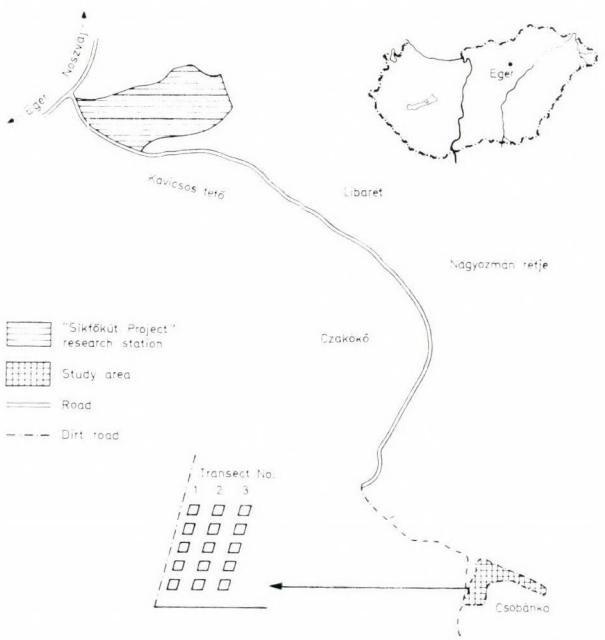

Fig. 1. Map of the study area showing the arrangement of transects and permanent quadrats

at an elevation of 200 m above sea level on a weak slope exposed to the south (PAPP and PRÉCSÉNYI 1980).

The area had been covered by a 70-years old sessile oak-turkey oak forest (*Quercetum petraeae-cerris*). The forest was cut down in 1979. The canopy cover of the forest was 80%. 85% of the trees was *Quercus cerris*, the others being *Quercus petraea*. In the shrub layer of 60% cover the dominant species were *Cornus mas*, *Crataegus monogyna*, *Crataegus oxyacantha*, *Ligustrum vulgare*, and *Quercus cerris*. The total cover of herbs was 35–40%. The cover of the following species was at least 15%: *Agrostis tenuis*, *Anthericum ramosum*, *Brachypodium silvaticum*, *Carex caryophyllaea*, *Filipendula vulgaris*, *Geum urbanum*, *Hieracium pilosella*, *Poa nemoralis*, *Viscaria vulgaris* and *Veronica officinalis*. The presence of some herbaceous species indicates mild acidity of the soil.

Methods

On July 21st, 1979, prior to deforestation, the floristic composition of the herb layer was determined (Table 1) and cover estimates for each species were recorded in five quadrats of 4×4 m^2 size.

In 1980, five permanent quadrats of 1 m^2 size were establisted in each of the three transects directed parallel to one another and also to the edge of the study area. Transect 1 was laid down at the edge of the former forest adjacent to a secondary grassland community. The other two transects were taken within the study area. A species list was drawn up and the percentage cover of each species was recorded for each permanent quadrat on July 20th, 1980, on July 23rd, 1981 and on July 10th, 1982 (Table 2).

Based on the 1980 and 1981 species lists, the quadrats were compared in every possible pair using Jaccard's index of similarity (cf. MUELLER-DOMBOIS and ELLENBERG 1974). The two resulting similarity matrices were subjected to cluster analysis. The dendrograms (Figs 2 and 3) show that quadrats from transects 2 and 3 are separated from those taken at the edge of the study area. Thus, the quadrats in transect 1 represent a different starting-point to the study of succession, compared to the others coming from inside the former forest.

Table 1

List of species found in the forest in an area of 80 m^2

Achillea collina	*Galeopsis pubescens*
Agrostis tenuis	*Geum urbanum*
Ajuga genevensis	*Hieracium bouhini*
Anthericum ramosum	*Hypericum perforatum*
Betonica officinalis	*Luzula albida*
Brachypodium silvaticum	*Phleum phleoides*
Calamintha clinopodium	*Poa nemoralis*
Carex michelii	*Polygonatum odoratum*
C. caryophyllea	*P. multiflorum*
Dactylis polygama	*Sedum maximum*
Euphorbia cyparissias	*Teucrium chamaedrys*
Festuca heterophylla	*Trifolium montanum*
F. valesiaca	*Veronica chamaedrys*
Filipendula vulgaris	*V. officinalis*
Fragaria vesca	*V. spicata*
Galium verum	*Viscaria vulgaris*

Table 2

Presence/absence data for species found in the transects in each year

	Transect 1			Transect 2			Transect 3		
	1980	1981	1982	1980	1981	1982	1980	1981	1982
Achillea collina	+	+	+	+	+	+	+	+	+
Agrimonia eupatoria	−	−	−	+	+	+	+	+	+
Agrostis tenuis	+	+	+	−	+	+	+	+	+
Agropyron repens	+	+	+	+	+	+	−	−	−
Ajuga genevensis	−	−	−	−	−	+	+	+	+
Anthericum ramosum	+	+	+	+	+	+	+	+	+
Anthoxanthum odoratum	+	+	+	+	+	−	−	−	−
Asperula cynanchica	+	+	+	−	−	−	−	−	−
Arenaria serpyllifolia	+	−	−	−	−	−	−	−	−
Atriplex tatarica	−	−	−	−	−	−	−	+	−
Brachypodium silvaticum	−	−	−	−	−	−	+	+	+
Calamintha clinopodium	−	−	−	−	−	+	−	−	−
Campanula sibirica	−	−	−	−	+	−	−	−	−
Carduus acanthoides	−	−	−	−	−	−	−	−	+
Carex caryophyllea	+	+	+	+	+	+	−	+	+
C. praecox	−	−	−	+	+	+	+	+	+
C. stenophylla	+	+	+	−	−	−	−	−	−
Carlina vulgaris	+	−	−	−	−	−	−	−	−
Centaurea micranthos	+	+	+	−	+	+	−	−	−
Centaurium minus	−	+	−	−	−	−	−	−	−
Cerastium caespitosum	+	−	−	−	−	−	−	−	−
C. viscosum	+	−	+	+	+	+	−	−	+
Cirsium arvense	−	−	−	+	+	+	+	+	+
C. vulgare	−	−	−	−	+	+	−	−	+
Convolvulus arvensis	−	−	−	−	−	+	−	−	−
Coronilla varia	−	−	−	+	+	+	−	−	+
Crataegus monogyna	+	+	+	+	+	+	+	+	+
Dantonia provincialis	+	+	+	+	+	+	+	+	+
Daucus carota	−	−	−	−	+	+	+	+	+
Dianthus pontederae	+	−	+	−	−	−	−	−	−
Dorycnium germanicum	−	−	−	+	+	+	−	−	−
Echinochloa crus-galli	−	−	−	−	−	−	+	−	−
Echium vulgare	+	+	−	−	−	+	−	−	−
Erigeron canadensis	−	+	−	+	+	+	+	+	+
Eryngium campestre	+	+	+	−	−	−	−	−	−
Euphorbia cyparissias	+	+	+	+	+	+	+	+	+
Euphrasia stricta	+	+	+	−	−	−	−	−	−
Festuca heterophylla	−	−	−	−	−	−	−	−	+
F. hirsuta et *valesiaca*	+	+	+	+	+	+	+	+	+
Filago arvensis	−	−	−	+	−	−	−	−	+
Filipendula vulgaris	+	+	+	−	+	+	+	+	+
Fragaria vesca	+	+	+	+	+	+	+	+	+
Galium mollugo	−	−	+	−	−	−	−	+	+
G. verum	+	+	+	+	+	+	+	+	+
Genista pilosa	+	+	+	−	−	+	−	−	−
Geum urbanum	+	−	−	+	+	+	+	+	+
Helianthemum ovatum	+	+	+	−	−	−	−	−	−
Hieracium bauhini	+	+	+	−	−	+	−	−	−
H. lachenalii	−	−	−	−	−	+	−	−	−
H. pilosella	+	+	+	−	+	−	−	−	−
Hypericum perforatum	+	+	+	+	+	+	−	−	−
Hypochoeris radicata	−	−	−	−	−	+	−	−	+
Koeleria glauca	+	+	+	−	−	−	−	−	−
Lactuca quercina	−	−	−	+	−	−	−	−	−
Leontodon hispidus	+	+	+	−	+	−	−	−	+

Table 2 (continued)

	Transect 1			Transect 2			Transect 3		
	1980	1981	1982	1980	1981	1982	1980	1981	1982
Lapsana communis	−	−	−	−	−	−	−	+	−
Ligustrum vulgare	−	−	−	+	+	+	+	+	+
Linaria vulgaris	−	−	−	+	−	−	−	−	−
Luzula campestris	+	+	+	−	−	−	−	−	−
Minuartia frutescens	−	−	−	−	−	−	−	−	+
Myosotis stricta	+	+	+	−	−	+	−	−	−
Orchis morio	−	−	+	−	−	−	−	−	−
Pimpinella saxifraga	−	−	−	+	−	−	−	−	−
Plantago lanceolata	+	+	+	−	−	−	−	−	+
Poa bulbosa	−	−	−	−	−	+	−	−	−
P. pratensis	−	−	−	+	+	+	−	−	+
P. compressa	+	+	+	+	+	+	+	+	+
Polygonum aviculare	−	−	−	+	+	−	−	−	−
P. convolvulus	−	−	−	+	+	+	+	+	+
Potentilla arenaria	+	+	+	+	+	+	−	+	−
P. argentea	−	+	+	−	−	+	+	+	+
Prunella vulgaris	−	+	+	−	−	−	−	−	−
Phleum phleoides	+	+	+	+	+	+	−	+	−
Pulsatilla nigricans	+	+	+	−	−	−	−	−	−
Quercus cerris	+	+	+	+	+	+	+	+	+
Rhinanthus major	+	+	+	−	−	−	−	−	−
Rosa sp.	+	+	+	+	+	+	−	−	+
Rumex acetosella	+	+	+	+	+	+	−	−	−
Saxifraga bulbifera	+	+	+	−	−	−	−	−	−
Scabiosa ochroleuca	+	−	−	−	−	−	−	−	−
Sedum acre	−	+	−	−	−	−	−	−	−
Seseli annuum	+	+	+	−	−	−	−	−	−
S. osseum	+	+	−	−	−	−	−	−	−
Setaria viridis	−	−	−	−	+	+	−	+	+
Silene otites	+	+	+	−	+	+	−	−	−
S. nutans	−	−	−	+	+	+	−	−	−
Solanum nigrum	−	−	−	+	+	−	−	−	−
Sonchus asper	−	−	−	+	−	−	−	−	−
Stellaria graminea	+	+	+	+	+	−	−	−	−
S. media	−	−	−	+	−	−	−	−	−
Taraxacum officinale	+	+	+	+	+	+	+	+	+
Teucrium chamaedrys	+	+	+	+	+	+	+	+	+
Thlaspi jankae	−	−	−	−	−	+	+	+	+
Thymus sp.	+	+	+	+	+	+	−	+	+
Trifolium alpestre	+	+	−	−	−	+	−	−	+
T. arvense	+	−	−	+	+	+	+	−	−
T. campestre	+	+	+	+	−	+	−	+	+
T. medium	−	+	−	−	−	−	−	−	−
T. montanum	+	+	+	+	−	+	−	−	−
Veronica chamaedrys	+	+	+	+	−	+	−	−	−
V. spicata	−	−	−	+	+	+	+	+	+
V. verna	+	+	−	−	−	−	−	−	−
Verbascum phoeniceum	+	+	+	+	+	+	+	+	+
Vicia cassubica	−	−	−	+	−	−	−	−	−
V. lathyroides	−	−	−	+	+	+	+	−	+
V. tenuifolia	−	−	−	+	−	−	−	−	−
V. tetrasperma	+	+	−	+	−	+	+	+	+
Viola hirta	+	+	+	+	+	+	+	+	+
V. kitaibeliana	−	−	−	+	+	+	+	+	+
V. silvestris	+	+	−	−	−	−	−	−	−
Viscaria vulgaris	+	+	+	+	+	+	+	+	+
Viola arvensis	−	−	−	−	−	−	−	−	+

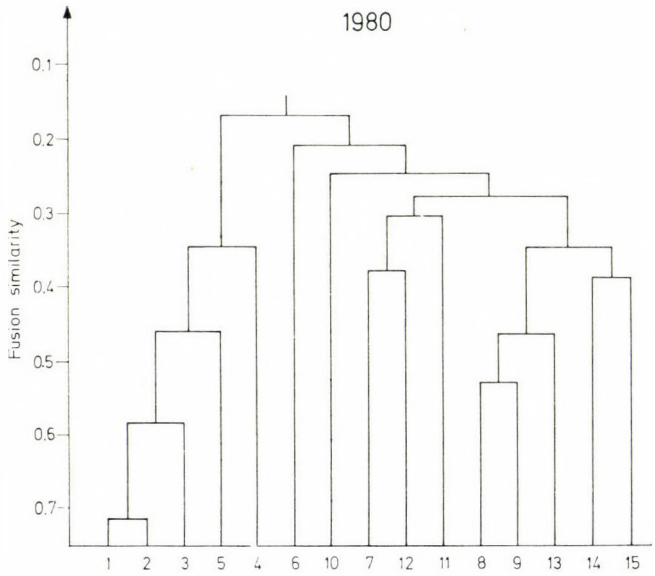

Fig. 2. Classification of quadrats based on the 1980 data. Transect 1: 1–5; transect 2: 6–10; transect 3: 11–15

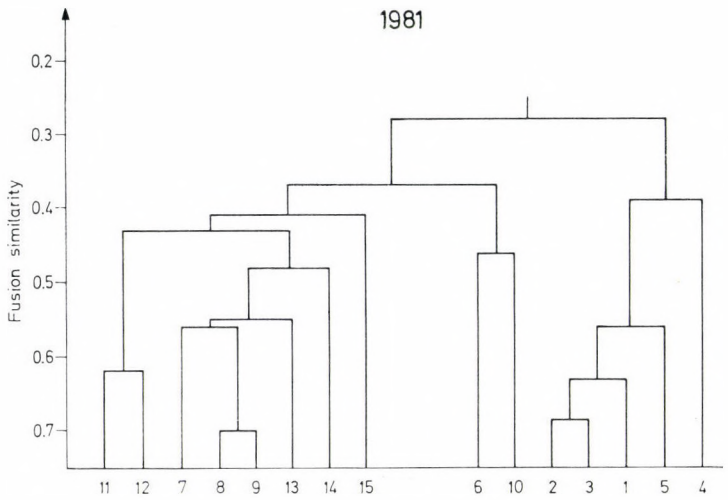

Fig. 3. Classification of quadrats based on the 1981 data. Transect 1: 1–5; transect 2: 6–10; transect 3: 11–15

Results

Floristical changes

In the understory vegetation of the forest seven species were found on the average per square meter. In the year following the deforestation the average number of species in the innermost transect (transect 3) was 16, next year 20, and 27 in 1982. In the quadrats of transect 2, the number of species significantly increased in the first year (26 species per quadrat), but in the next two years only a little change was observed (Table 3). The number of species in the quadrats of transect 1 was much higher than in the others in the first year (34 species per quadrat). Later this number did not increase further but decreased due to the disappearance of some species.

The species richness in the transects in 1980, 1981 and 1982, respectively, was the following: Transect 1: 63, 61, 55; transect 2: 55, 53 and 63; transect 3: 35, 41 and 52. That is, in transect 1 species richness decreased, whereas the opposite trend was observed in the inner transects.

The dynamics of vegetational change may be traced by determining the average number of species immigrated to, or disappeared from the quadrats (Fig. 4).

Transect 1 proved to be the most "stable". The average number of species present in its quadrats over three years was 26. This figure for transects 2 and 3 was only 17 and 13 respectively. In transect 1 the most significant species change was detected between 1980 and 1981: an average of 6 species disappeared from, and 3 new species occurred in each quadrat.

In transect 2 more changes were observed than in the first. Between 1980 and 1981 an average of 4 species occurred in each quadrat. The number of disappeared species was also 4. In 1982 six new species were found and three disappeared.

Table 3

The number of species in the permanent quadrats

		Quadrats Nos						Mean after transformation
		1	2	3	4	5	mean	
Transect 1	1980	38	34	41	29	30	34.4	5.65
	1981	35	32	37	27	26	31.4	5.59
	1982	35	31	33	27	30	31.2	5.53
								S.E.M. ± 0.17
Transect 2	1980	28	32	24	25	19	25.6	5.04
	1981	26	28	29	27	20	26.0	5.09
	1982	29	31	29	26	25	28.0	5.29
								S.E.M. ± 0.18
Transect 3	1980	18	18	18	11	14	15.8	3.96
	1981	22	21	23	17	16	19.6	4.44
	1982	27	32	24	25	26	26.8	5.17
								S.E.M. ± 0.16

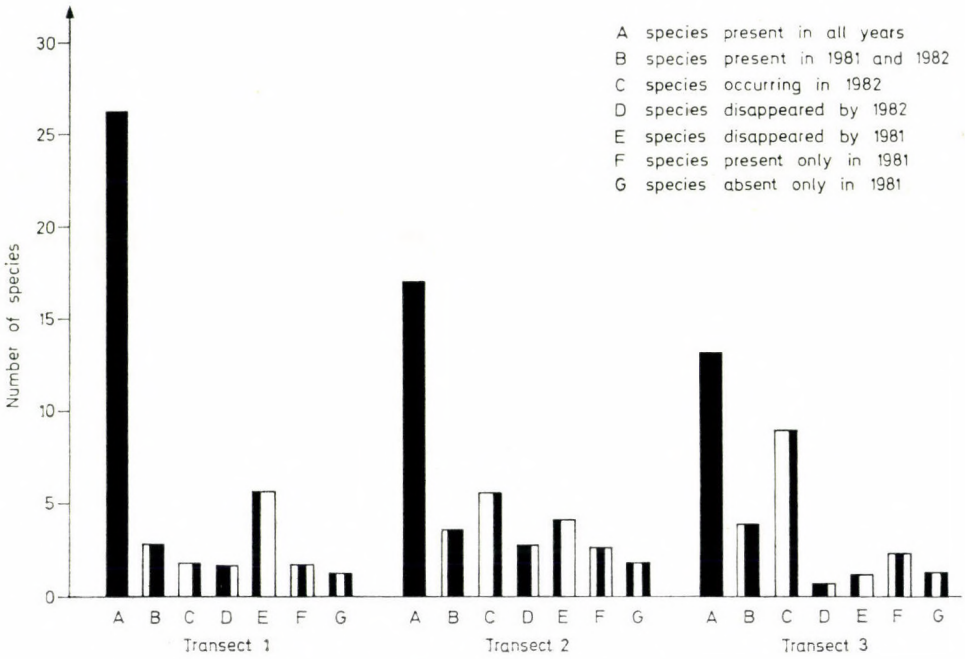

Fig. 4. Changes in the number of species in the transects

In 1981 only 4 new species appeared on the average in the quadrats of transect 3. This number was 9 next year.

The average number of species temporarily disappeared from, or occurred in the quadrats was relatively low (1–3) for all transects.

Table 4

The average cover, diversity and evenness for all transects

		Cover	N_0	N_1	N_2	N_∞	$E = (N_1/N_0) \times 100$
Forest	1979	39.0	6.6	11.92	9.34	5.17	69.3
Transect 1	1980	233.4	34.4	26.46	20.85	8.75	76.9
	1981	234.2	31.4	24.82	20.92	9.07	79.0
	1982	269.0	31.2	25.15	16.89	9.58	80.6
Transect 2	1980	206.6	25.6	19.27	14.93	7.06	75.3
	1981	221.8	26.0	20.14	15.60	7.49	77.5
	1982	253.0	28.0	21.22	14.14	9.69	75.8
Transect 3	1980	117.0	15.8	13.94	11.84	6.28	88.2
	1981	175.5	19.6	16.20	13.23	7.40	82.7
	1982	247.2	26.8	19.06	13.02	6.28	71.1

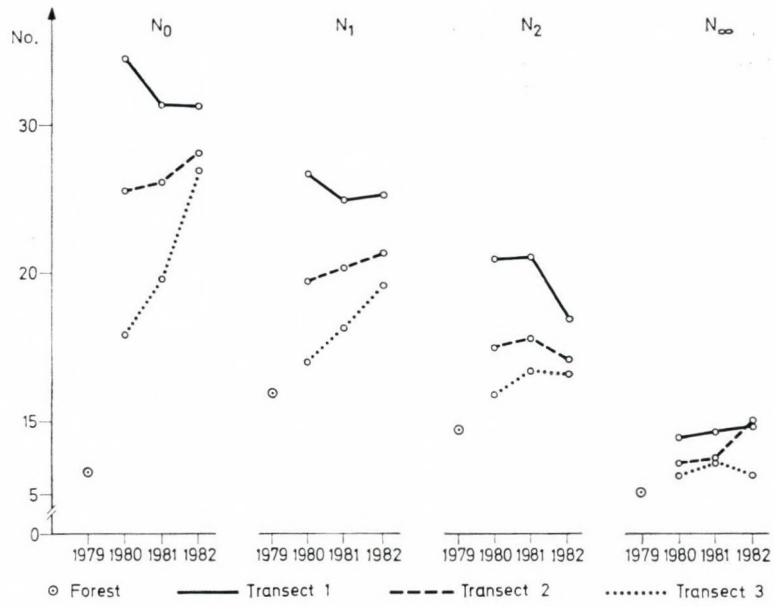

Fig. 5. Diversity changes in the transects

Changes in plant cover

In the previously forested area, sampled by transects 2 and 3, the reviving vegetation reached a cover 4.3 times higher than the original herb layer in 1980. Next year this factor was 5, and 6.4 after the third year (Table 4).

Of the dominant species in the forest only *Anthericum ramosum*, *Filipendula vulgaris* and *Veronica officinalis* maintained a cover of 15% or more in 1980, and also in 1981. *Agrostis tenuis* and *Carex caryophyllea* became dominant again only in 1981, whereas other species became more abundant than in the forest. These are *Achillea collina*, *Fragaria vesca*, *Galium verum* and *Festuca hirsuta*. Despite the fact that *Carex praecox*, *Cirsium arvense*, *Poa compressa* and *Rumex acetosella* were not present in the forest, they reached at least 15% cover in 1981. Next year the number of dominant species originally absent from the forest further increased, the new species being *Erigeron canadensis*, *Coronilla varia* and *Thymus* sp.

Most of the species with high cover values ($\leq$15%) in transect 1 were dominant also in the secondary grassland community. These are *Anthoxanthum odoratum*, *Agrostis tenuis*, *Danthonia provincialis*, *Hieracium pilosella*, *Carex praecox*, *Festuca hirsuta*, *Helianthemum ovatum*, *Poa compressa*, *Luzula campestris*, *Achillea collina* and *Phleum phleoides*.

The cover difference among transects has decreased considerably by the third year after cutting. In 1980 the average cover in the quadrats of transect 1 was 1.36 times higher than that in the other two, whereas in 1982 this value was only 1.07.

Diversity changes

The diversity values calculated based on Hill's functions (Hill 1973) are summarized in Table 4 and illustrated in Fig. 5. The values shown are within-transect averages.

The changes of N_0 (number of species) have already been discussed above.

The values of N_1 for the inner transects increased from the first year to the last. In the quadrats at the edge, this function had decreased by the year after cutting and slightly increased later. The most substantial change occurred in case of transect 3.

An initially slow increase is characteristic of the curves of N_2 which express dominance concentration. However, the value of this function decreased for all transects in 1982.

Function N_∞, which is the reciprocal value of the highest cover value, shows that in transects 1 and 2 the importance of species with extremely large cover is diminishing as succession progresses. However, in the quadrats of transect 3 low values were obtained again. This question will be discussed in detail in the next section.

The diversity curves tend to converge illustrating that the difference among transects disappear as succession progresses.

The N_1/N_0 ratio (evenness, E. HILL 1973) is the actual diversity expressed as the percentage of the maximum. It shows how close the given sampling unit is to the total disorder with respect to plant cover (Table 4).

In the quadrats of transect 1 the value of E slowly increased after deforestation indicating that the "steady-state" of the community was the least affected by disturbance in this case. In the quadrats of transect 3 there was a considerable increase in disorder in 1980, but a decrease was observed from 1981. There was a similar decrease in transect 3.

Dominance/diversity curves

Species composition and the dominance relations among species are consequences of resource partitioning and competition (cf. WHITTAKER 1965). For an appropriate characterization of diversity and dominance relations in a community, WHITTAKER (1965) suggests the use of productivity, phytomass and cover. Based on these quantities, dominance/diversity curves may be drawn whose shape reflects the partition of niche space by species, that is, the success of each species in competition (WHITTAKER 1965, PRÉCSÉNYI 1981).

In order to draw the curves the relative cover of each species was calculated based on the combined species list of each transect.

The dominance/diversity curve for transect 1 (Fig. 6) is of approximately sigmoid shape. The steepness of the uppermost section of the curve indicates the dominance of a single species, namely *Achillea collina*. Most of the other species are of medium importance and some others have little cover. For this reason, the lower part of the curve is steep again. In the next two years of succession the curves are almost linear since the importance of *Festuca hirsuta*, *Agrostis tenuis* and *Genista pilosa* increased and the dominance of *Achillea collina* decreased. This result implies that the niche space was relatively evenly partitioned among species in the second and third year. Curves of this type are characteristic of communities living in severe environmental conditions (WHITTAKER 1965).

The shape of dominance/diversity curves for transect 2 is sigmoid every year (Fig. 7). Parts in the niche space approximately similar in size are occupied by 2–3 species (*Fragaria vesca*, *Galium verum* and *Euphorbia cyparissias*). The flattened central part of the curves reflects the presence of numerous species of medium importance strongly competing with each other. The same species were found to be dominant every year. The three curves are very similar except that the lower section of the 1982 curve is more flattened than the others suggesting the occurrence of several, almost equally important species.

The curves for transect 3 in the first two years (Fig. 8) are steep and approximately linear. The third year of succession resulted in a sigmoid curve. Species with large cover are *Quercus cerris*, *Fragaria vesca* and *Euphorbia cyparissias*. The curves obtained for the first two years

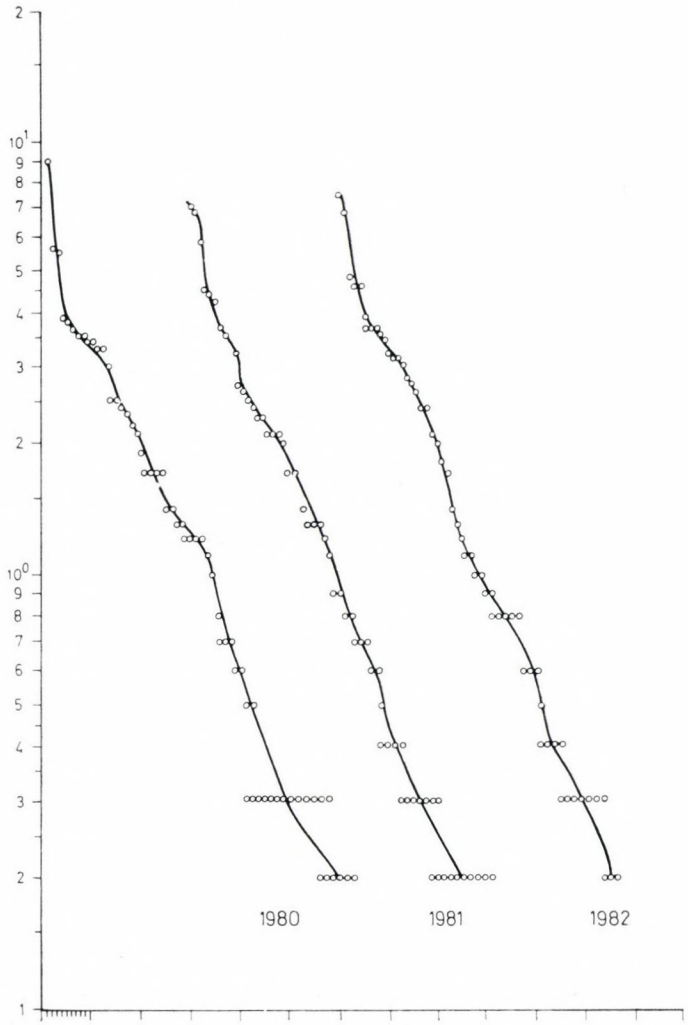

Fig. 6. Dominance/diversity curves for transect 1

of succession (when the total cover was the smallest) are similar to those obtained in weed communities and other open plant assemblages (cf. WHITTAKER 1965, PRÉCSÉNYI 1981). There was no species with extremely high cover value during the years of study.

Changes in plant strategies and life form composition

The life form composition of vegetation is closely related to plant strategies. MCARTHUR and WILSON (1967) introduced the concept of "r and K strategist" plants. The classification of plants based primarily on life-span and reproductive effort, i.e. on their position on the axis of the r–K continuum (MCNAUGHTON 1975), is comparable to GRIME's (1979) plant strat-

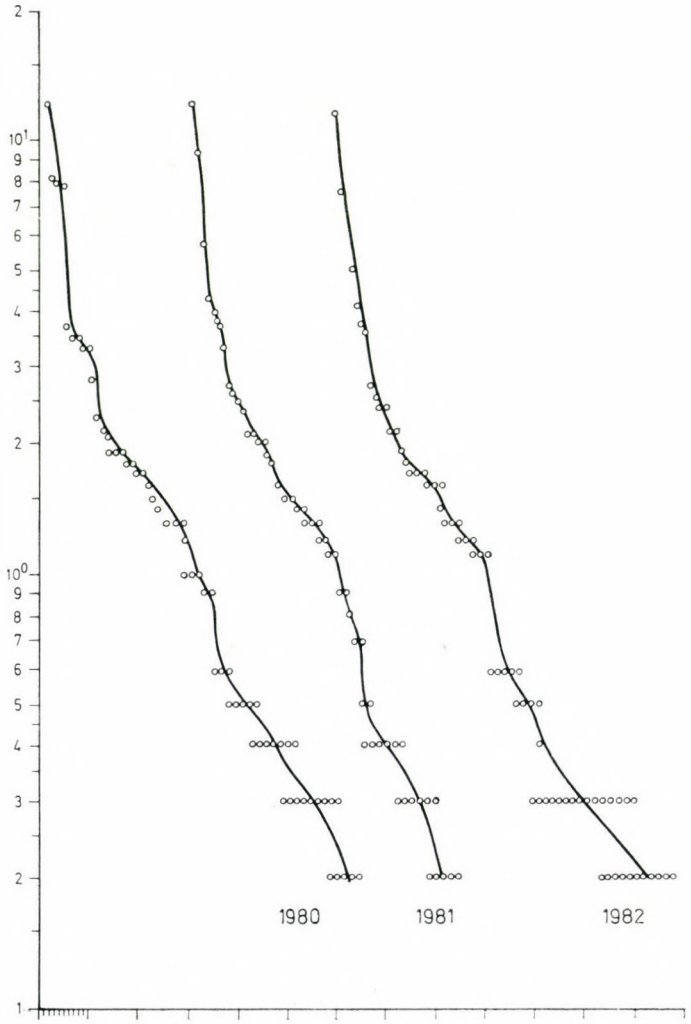

Fig. 7. Dominance/diversity curves for transect 2

egies. The ruderals (R) and stress tolerators (S) represent the extreme positions on the axis, whereas the competitors (C) are found in between. Having known the intermediate secondary strategies, the location of every species can be determined.

Most of the species appearing in the study area are ruderals, such as *Atriplex tatarica*, *Daucus carota*, *Erigeron canadensis*, *Lapsana communis*, *Setaria viridis* and *Viola kitaibeliana*. Others, e.g. *Campanula sibirica*, *Centaurea micranthos*, *Carex praecox*, *Hieracium pilosella*, *Leontodon hispidus*, *Prunella vulgaris*, *Sedum acre* and *Trifolium medium* belong to the C-S-R group. Most of the disappeared species are also C-S-R strategists. Some species remnant from the forest, such as *Brachypodium silvaticum*, are stress tolerators.

Lepš, Osbornova-Kosinova and Rejmanek (1982) claim that secondary succession usually starts with an assemblage consisting of r-strategists or ruderals. Grime (1979) explains

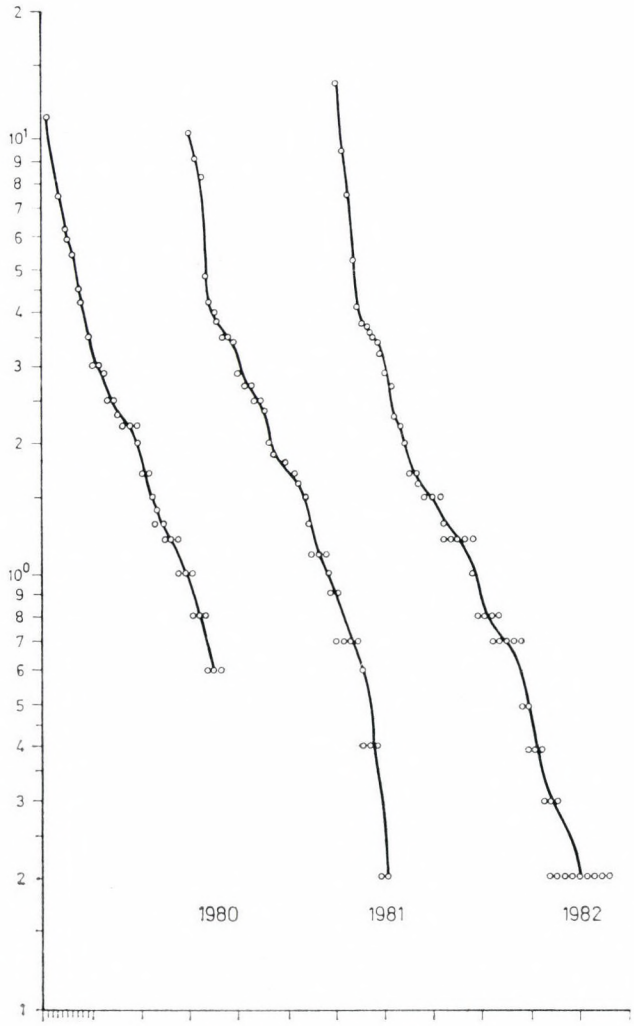

Fig. 8. Dominance/diversity curves for transect 3

that at the beginning of secondary succession the ruderals and competitors take a less prominent part in an inproductive environment than stress-tolerators. In the study area there was an outbreak of ruderals. The dominance of C-S-R strategists was also observed. In the future the expansion of perennials is expected, as it was already seen in 1982.

Life forms can be considered as strategies reflecting adaptation to macroclimate. In the study area 91% of the species in the herb layer were hemicryptophytes, geophytes and therophytes (Table 5). In the years following deforestation the percentage of these species dropped to 65–70% implying a 1/3–1/4 loss in proportion compared to 1979. At the same time the proportion of therophytes became 6–7 times higher than earlier. In transects 1 and 2 the proportion of annuals increased in 1980 and 1981, but decreased in 1982.

Table 5

Life form composition (%) and life form diversity in the transects

		H	G	TH	Th	M, MM, Ch	Diversity
Forest	1979	84	6	1	3	6	1.89
Transect 1	1980	68	5	2	13	12	2.57
	1981	67	6	2	12	13	2.80
	1982	70	7	3	7	13	2.37
Transect 2	1980	53	11	2	19	15	3.33
	1981	60	11	2	11	16	3.14
	1982	61	9	3	12	15	3.10
Transect 3	1980	54	11	5	18	12	3.34
	1981	48	12	6	20	14	3.86
	1982	54	8	8	18	12	3.60

H = hemicryptophytes; G = geophytes; TH = biennials; Th = therophytes; M, MM = phanerophytes; Ch = chamaephytes

Diversity was calculated for every quadrat according to HILL (1973) using five life form categories (see Table 5) and then the average diversity of each transect was examined. Similar trends were observed in transects 1 and 3: diversity first increased and later decreased. The highest diversity values were obtained for transect 3 every year supporting the previous observation that disorder is the highest in the innermost quadrats. The distribution of life forms is relatively low in transect 1 with diversity values between 2.3 and 2.8.

Table 6

Average percentages of diploid and polyploid species and the diploid/polyploid ratios

		Diploid	Polyploid	Diploid and polyploid	Diploid/polyploid ratio
		%			
Forest	1979	35.5	45.2	19.3	0.79
Transect 1	1980	42.9	46.5	10.6	0.92
	1981	38.3	50.3	11.4	0.76
	1982	38.4	46.8	14.8	0.82
Transect 2	1980	39.7	46.6	13.7	0.85
	1981	38.7	45.5	15.8	0.85
	1982	39.2	38.8	22.0	1.01
Transect 3	1980	43.6	44.5	11.9	0.98
	1981	49.4	38.5	12.1	1.28
	1982	47.6	38.0	14.4	1.25

The distribution of diploid and polyploid species

Several authors (e.g., HAGERUP 1932) suggest that there is a relationship between environment and the frequency of diploid and polyploid species. Polyploids are considered to be relatively common under extreme environmental conditions. Their morphological and physiological characteristics often reflect an increased adaptive capability (KOSTOV 1938, SCHWANITZ 1951). According to the results published by PIGNATTI (1960), the proportion of diploids seems to decrease as succession approaches climax.

The categorization of species follows, Soó (1966, 1968, 1970, 1973).

In this study the proportion of diploids and polyploids in the forest was 35.5% and 45.2%, respectively (Table 6). In the quadrats of transect 1, the diploid/polyploid ratio first decreased after cutting and then increased, but never reached 1. In transect 2 no significant change was seen. The diploid/polyploid ratio, falling within the interval (0.98, 1.25), increased in the quadrats of transect 3. In the inner quadrats this ratio was larger than that in the forest and in transect 1 in every case.

Summary

Concluding from the present results the secondary succession after deforestation may be characterized as follows.

The most striking fact is the significant increase of species number together with an increase in total cover. At the same time the number of individuals considerably increased as well. An evidence supporting this statement is that whereas species number was approximately quadruplicated, the total cover increased sixfold in three years. There was no species occupying an extremely large section of niche space. Instead, 3–4 dominant species of similar cover were present. Many species were found occupying similar, relatively medium sized portions of niche space. Several dominant species in the deforested area were remnants from the forest, others newly occurred and spread quickly as a result of environmental change. Another observation is that some species disappeared from the quadrats. Also, there were species occurring in, and disappearing from the transects temporarily. In every case the diversity was higher than in the forest.

The disorder of permanent quadrats was expressed in terms of evenness and life form diversity. Both measures indicated an initially increased disorder in the deforested area. In the second and third year of succession, however, decreasing trend in disorder was observed.

It was found that at the early stages of succession the number of diploid species increased at the account of polyploids.

The changes in the quadrats taken from the edge of the former forest were less significant than in the others. At the edge diversity was relatively high at the beginning of sampling, indicating an advanced stage of succession. A characteristic feature of the study area was that species composition and its change were determined primarily by the neighbouring secondary grassland. In these quadrats the disorder was always lower than inside the forest.

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STUDIES ON THE pH REQUIREMENT OF SOIL-INHABITING MUSHROOMS: THE R-SPECTRA OF MUSHROOM ASSEMBLAGES IN DECIDUOUS FOREST COMMUNITIES

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The scale of R-values for soil-inhabiting mushrooms is defined based on data from several years of sampling. The proportion of each category distinguished on the scale is determined for the mushroom assemblages of various forest soils based on production estimates. It was found that in very acidic soils the proportion of acidophilous plus acidofrequent species may be as high as 80–93%.

Introduction

There are several papers in the literature reporting pH measurements to describe the pH requirements of fungi (e.g. Hintikka 1960). However, additional studies are necessary to obtain an overall picture on the responses of fungi to the pH of the soil. An example illustrating the general situation is *Amanita rubescens*. Although it has been the subject of many studies, the diverse results suggest that the number of measurements done as yet is still insufficient. Modess (1941) considered *Amanita rubescens* as acidophilic on the basis of 73 measurements in Denmark. The pH of soils where this species was found ranged from 4.0 to 4.9. In Great Britain Grainger (1946) performed 21 measurements and concluded that the pH interval of *Amanita rubescens* is 4.0–5.8. In my examinations the pH range turned out to be 4.0–6.3 suggesting that this mushroom species is both acidophilous and subacidophilous.

The idea has emerged that new information may be gained using the cenological data obtained by Bohus and Babos (1960, 1967) through a relatively long period of time. As a consequence of climatic conditions, the forest soils of Hungary are fairly homogeneous as far as pH is concerned. pH is particularly homogeneous within the sample plots of 500 m² in which the soil samples were taken. Thus, reasonably precise estimates were obtained for the pH range of soils in the forest types examined allowing a detailed description of the pH requirements of mushrooms present in the forest stands.

Methods

The area of permanent plots was 500 m². Their shape was either a long rectangle (50 × 10 m) or a short rectangle (20 × 25 m) depending on field conditions. All "fruiting" bodies were collected within each plot and weighed. Based on several years of sampling the maximum production of each species was determined.

The soils were sampled and analysed for pH as follows. Soil samples were collected at each site where mushrooms were found, a 20 cm deep soil section was removed in each case and homogenized with boiled distilled water to reach a proportion of 1 : 2.5. The pH was measured using a combined glass electrode in the clear liquid above the deposition at the temperature of soil 16–18 hours after homogenization.

Results

The scale of R-values for mushrooms has been established by BOHUS and BABOS (1967) and BOHUS (1973). Its further refinement is done in the present study. The scale is described

Table 1

Classes on the scale of R-values

Class	Species	Occurrence in pH intervals	Occurrence
1A	Acidophilous I	3.7–4.8 (5.0)	Species occurring exclusively on highly acidic soils
1B	Acidophilous II	3.8–5.0 (5.5)	Mostly on highly soils between pH 3.8 and 5.0
2A	Acidophilous III acidofrequent	4.0–5.5	Species preferring highly acidic soils, but occurring also at pH between 5.0 and 5.5
2B	Acido-subacidophilous	4.0–6.3	Both on highly and weakly acidic soils
3	Subacidophilous	5.0–6.5	Most frequently on weakly acidic soils
4	Subacidoneutrophilous	(5.0) 5.3–7.2	On weakly acidic to neutral soils
5	Neutrobasophilous	6.5–8.2	Mainly on alkaline to neutral soils
6A	Subindifferent I	5.0–8.2	Species rather indifferent to soil reaction, on soils with pH between 5.0 and 8.2
6B	Subindifferent II	4.0–7.0	Species rather indifferent to soil reaction, on soils with pH between 4.0 and 7.0, rarely on more alkaline soils
6C	Indifferent	4.0–8.2	Species indifferent to soil reaction, on soils with pH between 4.0 and 8.2

Highly acidic soils: pH 3.7–5.0
Weakly acidic soils: pH 5.0–6.5
Neutral soils: pH about 7.0
Alkaline soils: pH above 7.2

and illustrated in Table 1 and Fig. 1. The species examined were assigned to the classes according to their pH requirements and tolerance (Tables 4 and 5).

The number of species belonging to each group on the scale of R-values is given below.

1A	Acidophilous I	42
1B	Acidophilous II	18
2A	(Acidophilous III (= acidofrequent)	24
2B	Acido-subacidophilous	42
3	Subacidophilous	40
4	Subacido-neutrophilous	6
5	Neutro-basophilous	12
6A	Subindifferent I	13
6B	Subindifferent II	13
6C	Indifferent	22

More than 70% of the species belong to the first three classes. In groups 4 and 5 only a few species are represented.

Table 2

The proportion of classes on the scale of R-values in different forest types. Results are expressed as percentages of the maximum "fruiting" body production

Forest type		Classes on the scale of R-values									
		1A	1B	2A	2B	3	4	5	6A	6B	6C
		%									
Vaccinium beechwood	Mátra Mts.: Nagylápafő	56	29	8	3					3	
Luzula beechwoods	Bakony Mts.: Farkasgyepü	46	23	11	19					1	
	Zemplén Mts.: Kiskerekhegy	47	13	10	25					3	1
	Visegrád Mts.: Nyalkabérc	16	3	49	28					5	
	Bükk Mts.: Samassahegy	11	3	53	25					7	
	Visegrád Mts.: Lomhegy	6	13	40	35	1				4	1
Dicranum beechwood	Visegrád Mts.: Nyalkabérc	25	21	24	16					4	
Luzula hornbeam oakwoods	Mátra Mts.: Parádsasvár	6	43	37	9					3	1
	Murarátka		56	26	9	2				5	2
	Visegrád Mts.: Helyiipari spring	9	26	15	41					7	2
Vaccinium oakwoods	Sopron Mts.: Nagykőhalom	11	73	2	13						
	Bükk Mts.: Balázshegy	27	16	32	20					4	1
Luzula oakwoods	Visegrád Mts.: Nyalkabérc		3	86	10						
	Visegrád Mts.: Nyalkabérc	3	9	64	17						
	Mátra Mts.: Murarátka		30	22	36	2			1	4	4
	Bükk Mts.: Samassahegy	5	10	29	27	3				24	2
	Visegrád Mts.: Lomhegy	1	19	9	59	1				9	1
Dicranum oakwood	Buda Mts.: Tökhegy	11	51	13	23					2	
Beechwood with a soil of more acidic character	Visegrád Mts.: Nyalkabérc		10	13	66					7	3
Hornbeam oakwood with a soil of more acidic character	Zemplén Mts.: Ósvavölgy	3	16	3	45	4	11		1	10	5

Table 2 (continued)

Forest type		Classes on the scale of R-values									
		1A	1B	2A	2B	3	4	5	6A	6B	6C
		%									
Quercus cerris-petraea forests	Bükk Mts.: Samassahegy			9	29	18				3	36
	Buda Mts.: Remetehegy			5	66	4			3	5	16
	Bükk Mts.: Balázshegy			1	33	3	27	1	3	25	6
Hornbeam-oakwoods	Buda Mts.: Tökhegy			5	61	9			2	16	6
Corydalis type	Bükk Mts.: Samassahegy				10	28			1	1	60
	Bükk Mts.: Balázshegy				24	43			4	10	19
Carex type	Bükk Mts.: Feketelen				39	26			23	5	6
	Samassahegy				50	41				7	
Asperula type	Visegrád Mts.: Helyiipari spring				75	4	14		2	1	3
Melica type	Visegrád Mts.: Helyiipari spring			1	50	6	34		1	4	4

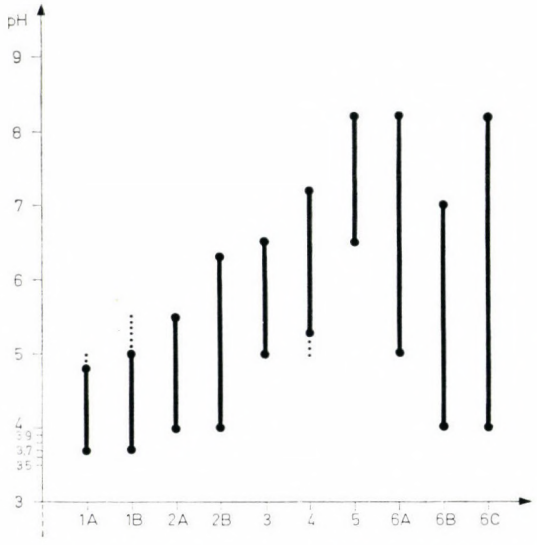

Fig. 1. Diagram illustrating the classes on the scale of R-values

Table 3

The proportion of combined groups on the scale of R-values in different forest types (cf. Table 2)

Forest types		Acidophilous classes, 1A + 1B + 2A	Indifferent classes, 6A + 6B + 6C
		%	
Vaccinium beechwood	Mátra Mts.: Nagylápafő	93	3
Luzula beechwoods	Bakony Mts.: Farkasgyepü	80	1
	Zemplén Mts.: Kiskerekhegy	70	4
	Visegrád Mts.: Nyalkabérc	68	5
	Bükk Mts.: Samassahegy	67	7
	Visegrád Mts.: Lomhegy	59	5
Dicranum beechwood	Visegrád Mts.: Nyalkabérc	80	4
Luzula hornbeam oakwoods	Mátra Mts.: Parádsasvár	86	4
	Murarátka	82	7
	Visegrád Mts.: Helyiipari spring	50	9
Vaccinium oakwoods	Sopron Mts.: Nagykőhalom	86	—
	Bükk Mts.: Balázshegy	75	5
Luzula oakwoods	Visegrád Mts.: Nyalkabérc	89	—
	Visegrád Mts.: Nyalkabérc	76	7
	Mátra Mts.: Murarátka	52	9
	Bükk Mts.: Samassahegy	44	26
	Visegrád Mts.: Lomhegy	29	10
Dicranum oakwood	Buda Mts.: Tökhegy	75	2
Beechwood with a soil of more acidic character	Visegrád Mts.: Nyalkabérc	23	10
Hornbeam oakwood with a soil of more acidic character	Zemplén Mts.: Ósvavölgy	22	16

Table 3 (continued)

Forest types		Acidophilous classes, 1A + 1B + 2A	Indifferent classes, 6A + 6B + 6C
		%	
Quercus cerris-petraea forests	Bükk Mts.: Samassahegy	9	43
	Buda Mts.: Remetehegy	5	22
	Bükk Mts.: Balázshegy	1	34
Hornbeam oakwoods	Buda Mts.: Tökhegy	5	24
Corydalis type	Bükk Mts.: Samassahegy	—	62
	Balázshegy	—	33
Carex type	Bükk Mts.: Feketelen	—	34
Carex type	Bükk Mts.: Samassahegy	—	7
Asperula type	Visegrád Mts.: Helyiipari spring	—	6
Melica type	Visegrád Mts.: Helyiipari spring	—	9

On the basis of measurements it is possible to determine the percentage of classes within the mushroom assemblages of various forest types (Table 2). Since the production was measured only for the "fruiting" bodies, the amount of mycelium spread beneath the soil was estimated. The comparison of classes was done on the basis of combined estimates. The results are summarized as follows.

1. In the forest types with very acidic soils, such as the beechwoods and oakwoods with *Luzula* or *Vaccinium*, 80–93% of the production is due to the acidophilous or acidofrequent species in many cases. These mushrooms, being all mycorrhizal, play an obviously important role in the forest ecosystem. On the contrary, in hornbeam-oakwoods and *Quercus petraea-cerris* forests with moderately acidic soil, the percentage of these classes in the total production was below 9. In the mesophilous forests with acidic soils intermediate percentages (22 and 23%) were obtained (Table 3, Fig. 2).

At the same time the indifferent species contribute very little (0–7%) to the production in the typical acidic forests, although they have equal chances in the competition with acidophilous species. The fact that the number of indifferent species is less than the half of the acidophilous plus acidofrequent species is only a partial explanation for this observation.

2. If the forest stands of acidic soils are ordered according to the percentages of acidophilous species, it is seen that the highest values (70–90%) were indicated in the most typical stands. In stands found at the border of the respective community this figure is less than 60%. Thus, these numerical values support the otherwise not easily documented observations made in the field.

In this sequence the most remarkable forest type is the *Vaccinium* beechwood at Nagylápafő in the Mátra Mountains. In this stand the proportion of acidophilous species reach the maximum, namely 93%.

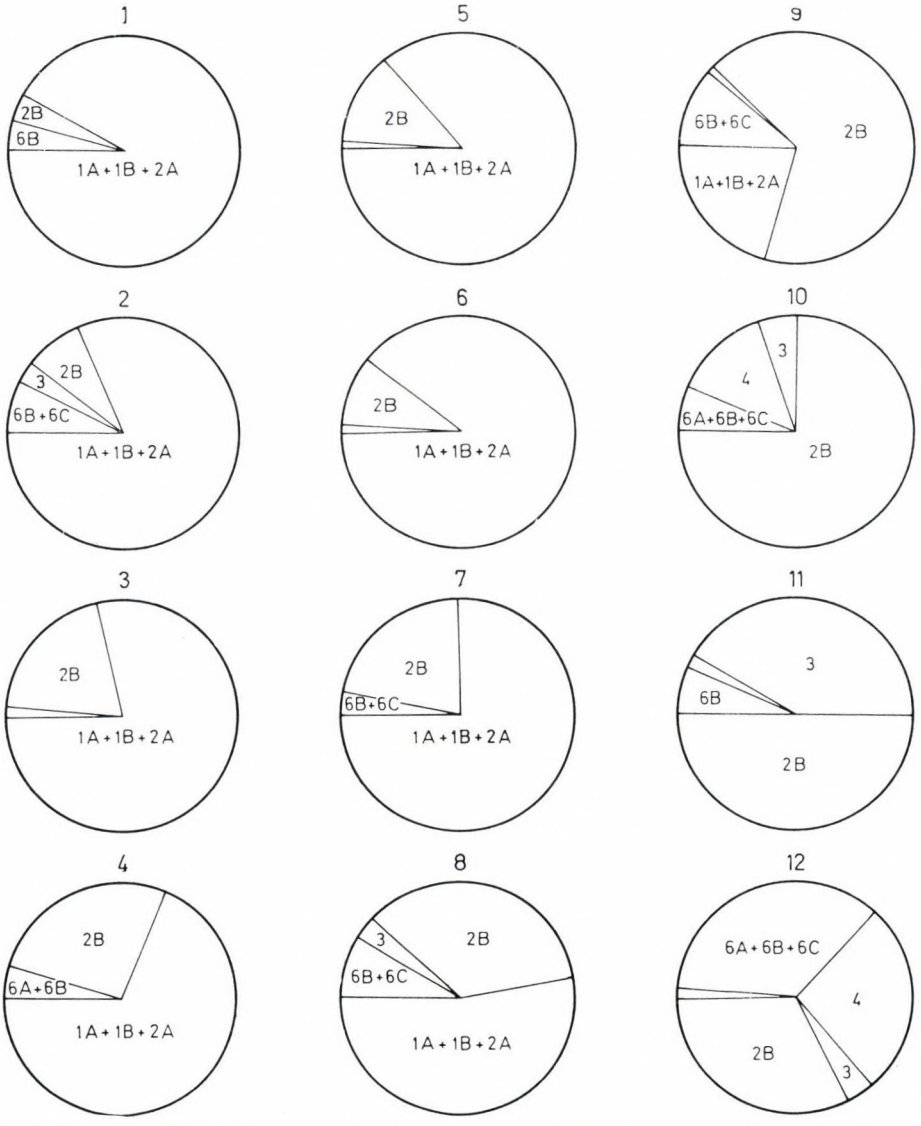

Fig. 2. Diagrams illustrating characteristic R-spectra of mushroom assemblages in different forest types: 1. *Vaccinium* beechwood: Mátra Mts.: Nagylápafő. 2. *Luzula* hornbeam oakwood: Murarátka, 3. *Luzula* beechwood: Bakony Mts.: Farkasgyepű. 4. *Luzula* beechwood: Visegrád Mts.: Nyalkabérc. 5. *Vaccinium* oakwood: Sopron Mts.: Kecskepatak valley. 6. *Luzula* oakwood: Visegrád Mts.: Nyalkabérc. 7. *Dicranum* oakwood: Buda Mts.: Tökhegy. 8. *Luzula* oakwood: Murarátka. 9. Beechwood with soil of more acidic character: Visegrád Mts.: Nyalkabérc. 10. *Asperula* hornbeam oakwood: Visegrád Mts.: Helyiipari spring. 11. *Carex* hornbeam oakwood: Bükk Mts.: Samassahegy. 12. *Quercus cerris-petraea* forest *Cladonia* facies: Bükk Mts.: Balázshegy

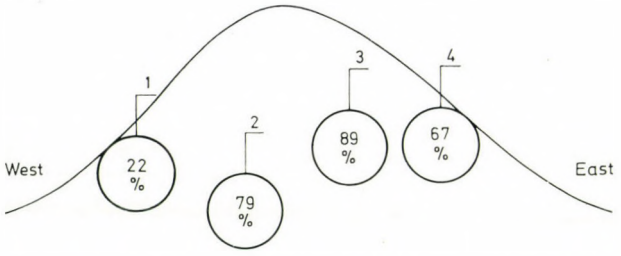

Fig. 3. Profile diagram showing the proportion of acidophilous plus acidofrequent species in the mushroom production of the forest types in Nyalkabérc, Visegrád Mts. 1 = Beechwood with a soil of more acidic character; 2 = *Dicranum* beechwood; 3 = *Luzula* oakwood; 4 = *Luzula* beechwood

3. In the *Luzula* oakwoods the percentage of acidophilous plus acidofrequent species is much less. On the other hand, the proportion of indifferent species increases as soon as the stands become more similar to the *Quercus petraea-cerris* forests in floristic composition. Similar statement holds for the *Luzula* hornbeam-oakwoods (represented by stands from Bükk Mts., Samassahegy, Visegrád Mts., Lomhegy and Helyiipari spring, cf. Table 3).

The proportion of acidophilous species (classes 1A, 1B and 2A) in the most intensively sampled area (Nyalkabérc, Visegrád Mts.) is illustrated by a diagram (Fig. 3).

Discussion

It was demonstrated by data that the species composition of soil-inhabiting mushroom assemblages of deciduous forests is mainly influenced by pH and community type. This statement also refers to the species indifferent to pH which account for 20% of the total mushroom flora. The explanation of this phenomenon needs further research. There is a tendency, for example, that *Gyroporus castaneus* found within a broad range of pH (4.2–8.2) is actually rare on very acidic soils in Hungary but usually present in neutral soils. Thus, despite its indifferent character, *Gyroporus castaneus* seems to prefer neutral pH conditions.

The presence of several so-called litter-inhabiting small fungi is not determined by forest type. Although these species are included in our cenological relevés they are not considered here because their annual production did not exceed 2 g/500 m² per species. The total weight of the "fruiting" bodies of these species was below $1^0/_{00}$ of the total production of fungi, therefore they appear to be of little importance in the life of soils.

A conclusion is that an indirect survey, such as the present study, may give an insight into the hidden life of forest soils and contribute much to the understanding of mechanisms that determine the presence and production of soil-inhabiting mushrooms.

Table 4

Group assignments for the species examined

	R		R
Agaricus abruptibulbus Peck	3	*C. auroturbinatus* (Secr.) Lge.	1B
A. bitorquis (Quel.) Sacc.	5	*C. balaustinus* Fr.	1A
A. bresadolianus Boh.	6A	*C. brunneo-fulvus* Fr.	2B
A. deylii Pil.	3	*C. bulliardi* (Fr.) Fr.	3
A. fusco-fibrillosus (Moell.) Pil.	3	*C. casimiri* (Vel.) Huijsm.	2A
A. haemorrhoidarius Kalchbr. et Schulz.	6C	*C. causticus* Fr.	1A
A. pseudopratensis Boh. var. *niveus* Boh.	5	*C. cotoneus* Fr.	6B
A. semotus Fr.	6B	*C. crassus* Fr. ss. Lge.	3
A. squamuliferus (Moell.) Moell.	4	*C. cristallinus* Fr.	1A
Agrocybe erebia (Fr.) Kühn.	3	*C. eburneus* (Vel.) Hry.	1A
A. praecox (Pers. ex Fr.) Fay.	3	*C. emollitus* Fr.	1A
Amanita aspera (Fr.) Hooker	3	*C. glaucopus* (Schff. ex Fr.) Fr.	2B
A. citrina (Schff.) S. F. Gray	2A	*C. glaucopus* (Schff. ex Fr.) Fr. var. *olivaceus* Mos.	2A
A. crocea (Quel.) Sing.	3	*C. hinnuleus* Fr.	2B
A. excelsa (Fr.) Bertillon	1A	*C. infractus* (Pers. ex Fr.) Fr.	6C
A. fulva (Schff. ex) Pers.	1B	*C. mucifluus* ss. Konr. et Maubl.	1A
A. gemmata (Fr.) Gill.	1A	*C. nemorensis* (Fr.) Lge.	2A
A. muscaria (L. ex Fr.) Hooker	1A	*C. olivascentior* R. Hry.	2A
A. pantherina (DC ex Fr.) Secr.	6B	*C. orellanus* (Fr.) Fr.	1A
A. phalloides (Vaill. ex Fr.) Secr.	6B	*C. pilatii* Svrcek	2A
A. rubescens (Pers. ex Fr.) Gray	2B	*C. privignoides* R. Hry.	1B
A. strobiliformis (Vitt.) Quél.	5	*C. purpurascens* Fr. var. *largusoides* Hry.	2A
Boletus aereus Bull. ex Fr.	1A	*C. renidens* Fr.	1A
B. aestivalis Paulet ex Fr.	1B	*C. rigentoides* Boh.	3
B. calopus Fr.	1A	*C. rufoolivaceus* Fr.	3
B. luridus Schff. ex Fr.	6C	*C. torvus* (Bull. ex Fr.) Fr.	1B
B. pinicola Vitt.	1A	*C. triumphans* ss. Lge.	1A
B. queletii Schulz.	3	*C. trivialis* Lge.	6B
B. rhodoxanthus (Krbh.) Kbch.	3	*C. venetus* (Fr. ex Fr.) Fr.	2A
B. regius Krbch.	2A	*C. vibratilis* (Fr.) Fr.	1A
B. torosus Fr.	1B	*C. xanthophyllus* Cke.	1A
Calocybe ionides (Bull. ex Fr.) Donk	3	*Craterellus cornucopioides* Pers.	2B
Caloporus cristatus (Pers.) Quel.	1A	*C. sinuosus* Fr.	2B
C. pes-caprae (Pers.) Pil.	1A	*Dermocybe cinnabarina* (Fr.) Wünsche	2B
Cantharellus cibarius Fr.	2A	*D. cinnamomeolutea* (Orton) Mos.	1A
C. cibarius Fr. f. *pallidus* R. Sch. in Mich. Schulz.	3	*D. croceifolia* (Peck) Mos.	1A
C. cinereus Fr.	2B	*D. phoenicea* (Bull. ex Mre.) Mos.	1A
C. tubaeformis Fr.	1A	*Gyroporus castaneus* (Bull. ex Fr.) Quel.	6C
Chalciporus piperatus (Bull. ex Fr.) Bat.	1A	*Hebeloma crustuliniforme* (Bull. ex Fr.) Quel.	6A
Clavariadelphus pistillaris (Fr.) Donk	2B	*H. edurum* Metr.	5
Clavulina cristata (Fr.) Schroet.	2B	*H. pumilum* Lge.	1A
Clitocybe geotropa (Bull. ex Fr.) Quel.	4	*H. sarcophyllum* (Peck) Sacc.	3
C. gibba (Pers. ex Fr.) Kummer	6B	*H. subcaespitosum* Bon	5
C. inornata (Sow. ex Fr.) Gill.	6C	*Hydnellum velutinum* (Fr.) Karst.	1A
C. odora (Bull. ex Fr.) Kummer	3	*Hydnum repandum* L. ex Fr.	2A
Clitopilus prunulus (Scop. ex Fr.) Kummer	2B	*Hygrophorus eburneus* (Bull. ex Fr.) Fr.	6B
Collybia butyracea (Bull. ex Fr.) Quel.	6B	*H. leucophaeus* (Scop. ex Fr.) Fr.	3
Coprinus picaceus (Bull.) Fr.	6C	*H. nemoreus* (Lasch) Fr.	1A
Cortinarius amarescens (Mos.) Mos.	1A	*H. penarius* Fr.	3
C. anomalus (Fr. ex Fr.) Fr.	2B	*H. russula* (Schff. ex Fr.) Quel.	2A

Table 4 (continued)

	R		R
Inocybe asterospora Quel.	2B	*Macrolepiota procera* (Scop. ex Fr.) Sing.	6C
I. caesariata (Fr.) Karst.	5	*M. rhacodes* (Vitt.) Sing.	4
I. corydalina Quel.	3	*Melanoleuca melaleuca* (Pers. ex Fr.) Mre.	4
I. descissa (Fr.) Quel.	6B	*Morchella conica* Pers.	5
I. fastigiata (Schff. ex Fr.) Quel.	6A	*M. esculenta* Pers. ex St. Amans	5
I. geophila (Sow. ex Fr.) Kummer	3	*Mycena epipterygia* (Scop. ex Fr.) S. F. Gray	1A
I. godeyi Gill.	5	*M. galopoda* (Pers. ex Fr.) Kummer	2A
I. jurana Pat.	3	*M. pelianthina* (Fr.) Quel.	3
I. lanuginella (Schroet. ap Cohn) Konr. et Maubl.	6A	*M. pura* (Pers. ex Fr.) Kummer	6C
I. ovatocystis Kühn.	1A		
I. patouillardi Bres.	4		
I. pyriodora (Pers. ex Fr.) Quel.	3		
		Otidea onotica (Pers.) Fuck.	2A
Laccaria amethystina (Bolt. ex Hooker) Murr.	2A	*Oudemansiella platyphylla* (Pers. ex Fr.) Mos.	3
L. laccata (Scop. ex Fr.) Bk. et Br.	6B		
Lactarius acerrimus Britz.	6A	*Paxillus involutus* (Batsch) Fr.	6C
L. acris Bolt. ex Fr.	1A	*Phallus impudicus* L. ex Pers.	6C
L. aspideus Fr. var. *flavidus* Boud.	6A	*Phellodon confluens* (Pers.) Pouz.	1A
L. azonites Bull. ex Fr.	3	*Pholiota lenta* (Pers. ex Fr.) Sing.	3
L. blennius Fr.	2B	*Pulveroboletus cramesinus* (Secr.) Sing.	2B
L. camphoratus (Bull. ex) Fr.	1A		
L. chrysorrheus Fr.	1B		
L. circellatus Fr.	3	*Ramaria aurea* (Fr.) Quel.	1A
L. decipiens Quel.	2B	*R. botrytis* (Fr.) Rick.	1A
L. ichoratus Batsch ex Fr. ss. lat.	6C	*R. fennica* (Karst.) Rick.	1A
L. insulsus Fr.	4	*R. flava* (Fr.) Quel.	1A
L. mairei Mal.	5	*R. formosa* (Fr.) Quel.	1B
L. pallidus Pers. ex Fr.	2B	*Rhodophyllus clypeatus* (L. ex Fr.) Sing.	6A
L. piperatus (L. ex Fr.) S. F. Gray	2B	*R. nidorosus* (Fr.) Quel.	6C
L. pterosporus Romagn.	2B	*R. rhodopolius* (Fr.) Quel.	3
L. quietus Fr.	2B	*R. sinuatus* (Bull. ex Fr.) Sing.	3
L. serifluus DC ex Fr.	2B	*Ripartites tricholoma* (A. et S. ex Fr.) Karst.	2B
L. uvidus Fr.	2A	*Rozites caperata* (Pers. ex Fr.) Karst.	1B
L. vellereus (Fr.) Fr.	2A	*Russula acrifolia* Romagn.	2B
L. volemus Fr.	2B	*R. atropurpurea* Krbh.	2B
Leccinum crocipodium (Let.) Watl.	2B	*R. aurata* (With.) ex Fr.	2B
L. griseum (Quel.) Sing.	2B	*R. chamaeleontina* (Fr.) Fr. ss. Romagn.	2B
L. quercinum (Pil.) Pil.	1A	*R. cyanoxantha* Schff. ex Fr.	2B
Lepiota aspera (Pers. in Hofm. ex Fr.) Quel.	6A	*R. decipiens* (Sing.) Kühn. et Romagn.	6C
L. clypeolaria (Bull. ex Fr.) Kummer	6C	*R. delica* Fr. var. *trachyspora* Romagn.	2A
L. cristata (A. et S. ex Fr.) Kummer	6C	*R. emetica* Fr.	1B
Lepista luscina (Fr.) Sing.	6A	*R. farinipes* Rom. apud Britz.	2B
Leucocoprinus badhamii (Bk. et Br.) Mos.	5	*R. fellea* Fr.	1B
L. pilatianus (Demoulin) Bon et Boiffard	5	*R. foetens* Fr.	6B
Leucocortinarius bulbiger (A. et S. ex Fr.) Sing.	6B	*R. fragilis* (Pers. ex Fr.) Fr.	2B
Leucopaxillus giganteus (Fr.) Sing.	3	*R. heterophylla* (Fr.) Fr.	2B
Lycoperdon echinatum Pers.	3	*R. lactea* (Pers.) Fr. ss. Sing.	1B
L. foetidum Bon	1A	*R. laeta* J. Schff.	3
L. molle Pers.	6C	*R. laurocerasi* Melz.	2B
L. perlatum Pers.	6C	*R. lepida* Fr.	2A
Lyophyllum infumatum (Bres.) Kühn.	1B	*R. lilacea* Quel.	3
L. transforme (Britz.) Sing.	1A	*R. luteotacta* Rea	6C
		R. maculata Quel. et Roz.	6C
		R. nigricans (Bull.) Fr.	1B

Table 4 (continued)

	R		R
R. ochroleuca (Pers.) Fr.	3	*Tricholoma acerbum* (Bull. ex Fr.) Quel.	1B
R. odorata Romagn.	2B	*T. album* (Schff. ex Fr.) Quel.	6C
R. olivacea (Schff. ex Secr.) Fr.	2A	*T. columbetta* (Fr.) Kummer	1A
R. pectinatoides Peck	3	*T. orirubens* Quel.	3
R. persicina Krbh. em. Melz. et Zv.	3	*T. saponaceum* (Fr.) Kummer	6B
R. purpurata Crawshay	2B	*T. scalpuratum* (Fr.) Quel.	6C
R. romellii R. Mre. ss. str.*	2A	*T. sciodes* (Secr.) Mart.	1B
R. romellii R. Mre.	2B	*T. sejunctum* Sow. ex Fr.) Quel.	2B
R. rosea Quel.	2A	*T. sulphureum* (Bull. ex Fr.) Kummer	2B
R. rutila Romagn.	3	*T. ustale* (Fr. ex Fr.) Kummer	1B
R. solaris Ferd. et Winge	2A	*T. ustaloides* Romagn.	1B
R. sororia (Fr.) Romell ss. Boud.	3		
R. vesca Fr.	2B	*Xerocomus chrysenteron* (Bull. ex St. Amans) Quel.	6A
R. vinosopurpurea J. Schff.	3	*X. chrysenteron* (Bull. ex St. Amans) Quel. var. *acidophilus* Boh.	1A
R. virescens (Schff. ex Zant.) Fr.	2B	*X. rubellus* (Krbh.) Quel.	4
Strobilomyces floccopus (Vahl in Fl. Dan. ex Fr.) P. Karst.	2A	*X. subtomentosus* (L. ex Fr.) Quel.	2B

* *romellii* ss. str. (= var. *chlorina* in herb.): cap ± green

Table 5

Number of occurrences for each species and all pH-intervals

	Occurrence number of stands			Usual pH of the actual community type	Measured soil pH values
	acido-philic forests	sub-acido-philic forests	neutro-baso-philic forests		
			R: 1A		
Amanita excelsa	10			4.0–4.8	
A. gemmata	6			4.0–4.8	
A. muscaria	27			3.8–4.8	3.7, 4.0, 4.1, 4.2, 4.2
Boletus aereus	6			4.0–4.8	
B. calopus	16			4.0–4.8	4.1, 4.2, 4.7
B. pinicola	4			4.0–4.8	4.1
Caloporus cristatus	24			3.8–4.7	4.2
C. pes-caprae	6			3.8–4.5	
Cantharellus tubaeformis	30			3.7–4.5	
Chalciporus piperatus	15			3.8–4.5	3.9, 4.1, 4.1
Cortinarius amarescens	8			4.0–4.8	
C. balaustinus	5			3.8–4.7	
C. causticus	15	1*		4.0–4.8	4.8
C. eburneus	7			4.0–4.8	
C. emollitus	12			3.8–4.7	
C. mucifluus ss. konr. et Maubl.	16			4.0–5.0	4.1, 4.1, 4.5
C. orellanus	12			4.0–4.9	4.1, 4.2, 4.5, 4.9
C. renidens	13			4.0–4.7	4.1, 4.4, 4.7
C. triumphans ss. Lge.	16	1*		4.0–5.0	
C. vibratilis	34			3.8–4.7	3.8
C. xanthophyllus	8			3.8–4.7	
Dermocybe cinnamomeolutea	7			4.0–4.7	
D. croceifolia	8			4.0–4.7	
D. phoenicea	29			3.8–4.5	3.8, 3.9, 4.0, 4.1, 4.2
Hebeloma pumilum	10			4.0–4.7	
Hydnellum velutinum	16			3.8–4.7	
Hygrophorus nemoreus	14			4.0–4.7	4.1
Inocybe ovatocystis	10			4.0–4.7	
Lactarius acris	10			4.0–5.0	
L. camphoratus	41			3.7–4.7	4.0, 4.1, 4.1
Leccinum quercinum	9			4.0–4.7	4.0, 4.0, 4.2, 4.5
Lycoperdon foetidum	9			4.0–5.0	
Lyophyllum transforme	14	1*		4.0–5.0	
Mycena epipterygia	15	1*		4.0–5.0	
Phellodon confluens	9			3.8–4.5	
Ramaria aurea	10			3.8–4.5	
R. botrytis	18			3.8–4.5	4.2
R. fennica	5			3.8–4.5	
R. flava	13			3.8–4.5	4.4
Rozites caperata	14	2*		3.5–4.8	3.5, 3.9, 4.2, 4.5
Tricholoma columbetta	15			4.0–5.0	4.1, 4.2, 4.3
Xerocomus chrysenteron var. *acidophilus*	13			4.0–4.7	4.1, 4.3, 4.3

Table 5 (continued)

	Occurrence number of stands			Usual pH of the actual community type	Measured soil pH values
	acido-philic forests	sub-acido-philic forests	neutro-baso-philic forests		
			R: 1B		
Amanita fulva	11	2		3.9–5.0 (–5.5)	3.9, 3.9, 4.2, 4.5
Boletus aestivalis	48	7		4.0–5.0 (–5.5)	4.2, 4.2, 4.2, 4.3, 4.4, 4.5, 4.7, 5.0, 5.5
B. torosus	6	1		4.0–5.0 (–5.2)	
Cortinarius auroturbinatus	17	2		4.3–5.0 (–5.3)	
C. privignoides	17	2		4.0–5.0 (–5.3)	
C. torvus	48	5		3.7–5.0 (–5.3)	3.7, 3.9, 4.1, 4.2
Inocybe petiginosa	17	3		4.0–5.0 (–5.5)	
Lactarius chrysorrheus	26	3		3.9–5.0 (–5.2)	3.9, 4.1, 4.3, 5.0, 5.1, 5.2, 5.2
Lyophyllum infumatum	8	1		4.0–5.0 (–5.2)	
Ramaria formosa	32	3		4.0–5.0 (–5.5)	4.2
Russula emetica	52	5		3.8–4.5 (–5.3)	3.8, 4.2, 5.3
R. fellea	42	2		3.8–5.0 (–5.3)	4.1, 4.3
R. lactea ss. Sing.	6	1		4.3–5.0 (–5.2)	
R. nigricans	40	5		3.9–5.0 (–5.3)	3.9, 4.1, 4.2, 4.3, 4.9, 4.9, 5.2, 5.3
Tricholoma acerbum	22	2		4.0–5.0 (–5.2)	4.2
T. sciodes	21	2		4.0–5.0 (–5.2)	4.1, 4.2, 4.5
T. ustale	32	4		4.0–5.0 (–5.5)	4.1, 4.2, 4.5, 5.5
T. ustaloides	16	2		4.0–5.0 (–5.2)	
			R: 2A		
Amanita citrina	48	16		4.0–5.5	3.9, 4.1, 4.2, 4.5, 5.0, 5.5
Boletus regius	12	5		4.0–5.5	
Cantharellus cibarius	47	17		4.0–5.6	4.1, 4.1, 4.2, 4.5, 4.9, 4.9, 5.1, 5.6, 5.6
Cortinarius casimiri	9	4		4.0–5.5	
C. glaucopus var. *olivaceus*	10	3		4.3–5.6	
C. nemorensis	27	8		4.2–5.5	4.3, 4.4, 4.5
C. olivascentior	15	5		4.2–5.5	
C. purpurascens var. *largusoides*	26	8		4.0–5.2	4.1, 4.5
C. venetus	11	4		4.2–5.5	
Hydnum repandum	40	14		4.0–5.5	3.9, 4.1, 4.8
Hygrophorus russula	17	6		4.0–5.5	4.2, 4.5
Laccaria amethystina	25	8		4.0–5.3	4.1, 4.1, 4.4
Lactarius uvidus	16	5		4.2–5.5	
L. vellereus	42	12		4.0–5.6	4.1, 4.2, 5.0, 5.2, 5.3, 5.5
Mycena galopoda	14	5		4.2–5.5	
Otidea onotica	8	4		4.0–5.5	
Russula delica var. *trachyspora*	20	8		4.0–5.5	4.1, 4.7, 4.8, 4.9
R. lepida	41	20		4.0–5.5	4.0, 4.3, 4.8, 5.0, 5.2, 5.2, 5.2, 5.3, 5.4
R. olivacea	21	7		4.3–5.7	5.5, 5.7
R. romellii ss. str.	21	5		4.2–5.5	
R. rosea	18	6		4.0–5.5	4.6, 4.9
R. solaris	12	5		4.0–5.5	5.2
Strobilomyces floccopus	12	5		4.0–5.3	4.1, 4.1, 4.1, 4.2, 4.3, 4.5

Table 5 (continued)

	Occurrence number of stands			Usual pH of the actual community type	Measured soil pH values
	acido-philic forests	sub-acido-philic forests	neutro-baso-philic forests		
			R: 2B		
Amanita rubescens	49	22		4.0–6.3	3.9, 4.2, 4.4, 5.1, 5.1, 6.0, 6.2
Cantharellus cinereus	16	14		4.0–6.0	
Clavariadelphus pistillaris	7	23		4.2–6.3	
Clavulina cristata	19	30		4.0–6.3	
Clitopilus prunulus	17	20		4.3–6.3	
Cortinarius anomalus	18	14		4.0–6.3	
C. brunneo-fulvus	24	23		4.2–6.3	
C. glaucopus	8	14		4.3–5.8	5.5
C. hinnuleus	26	27		4.0–6.3	5.4
C. pilatii	10	3		4.0–5.5	
Craterellus cornucopioides	46	33		4.0–5.8	4.5, 4.5, 4.5, 4.6, 4.7, 5.4
C. sinuosus	28	20		4.0–6.0	
Dermocybe cinnabarina	4	3		4.2–5.8	
Inocybe asterospora	35	14		4.2–6.3	
Lactarius blennius	39	26		4.0–6.0	4.8
L. decipiens	16	20		4.2–6.0	4.2, 4.3, 4.7, 5.7, 6.0, 6.1
L. pallidus	25	20		4.0–6.0	
L. piperatus	26	27		4.0–6.3	4.5, 4.9, 5.0
L. pterosporus	11	10		4.0–5.8	
L. quietus	18	33		4.0–6.3	3.7, 4.2, 4.3, 4.8, 6.0, 6.1, 6.4
L. serifluus	22	36		4.0–6.3	5.8
L. volemus	24	18		4.0–6.0	4.9, 4.9
Leccinum crocipodium	5	7		4.2–5.8	4.7, 5.0, 5.8
L. griseum	16	27		4.0–6.3	
Pulveroboletus cramesinus	3	3		4.0–5.8	
Ripartites tricholoma	9	17		4.3–6.3	
Russula acrifolia	5	6		4.0–6.3	4.1, 4.3, 5.7, 6.1, 6.3
R. atropurpurea	27	18		4.2–5.8	4.3, 5.0, 5.3
R. aurata	7	15		4.3–6.0	5.3, 5.9
R. chamaeleontina	39	38		4.2–6.3	4.3, 5.0, 5.1, 5.7, 5.8
R. cyanoxantha	44	43		4.2–6.2	4.3, 5.0, 5.2, 5.3, 5.6, 5.6, 6.1, 6.4
R. farinipes	4	5		4.3–6.3	
R. fragilis	28	30		3.7–5.8	3.5, 4.1, 4.2, 4.3, 4.4, 4.4, 4.5, 5.2, 5.2
R. heterophylla	11	28		4.3–6.3	5.0, 5.2, 5.6, 6.4
R. laurocerasi	7	8		4.3–6.3	4.5, 5.4
R. odorata	12	21		4.3–6.0	6.0
R. purpurata	5	8		4.2–6.3	
R. romellii	20	33		4.2–6.3	
R. vesca	33	28		3.8–5.8	3.9, 3.9, 4.5, 4.9, 5.4
R. virescens	20	17		4.0–5.8	4.2, 4.7, 4.8, 5.1, 5.3
Tricholoma sejunctum	12	7		4.2–6.0	
T. sulphureum	16	20		4.2–6.3	
Xerocomus subtomentosum	21	35		4.0–6.0	4.2, 4.9, 4.9, 5.0, 5.5

Table 5 (continued)

	Occurrence number of stands			Usual pH of the actual community type	Measured soil pH values
	acido-philic forests	sub-acido-philic forests	neutro-baso-philic forests		
			R: 3		
Agaricus abruptibulbus	2	32		(4.5–) 5.0–6.5	4.4, 5.9
A. fusco-fibrillosus		7		5.3–6.5	
Agrocybe erebia	1	10		(4.7–) 5.0–6.5	6.5
A. praecox		19		5.5–6.5	
Amanita aspera	3	16		(4.5–) 5.0–6.5	4.9, 5.3, 5.7, 5.9
A. crocea		7		5.0–6.5	5.5, 5.6, 5.8, 5.9, 6.2
Boletus queletii	1	8		(4.5–) 5.0–6.5	5.9
B. rhodoxanthus	1	8		(4.5–) 5.0–6.5	
Calocybe ionides		11		5.0–6.2	
Cantharellus cibarius f. *pallidus*		8		5.0–6.5	5.1, 5.3, 5.9, 6.4
Clitocybe odora	5	33		5.0–6.5	
Cortinarius bulliardi	3	12		(4.5–) 5.0–6.5	
C. crassus		11		5.0–6.0	
C. rigentoides		16		5.0–6.5	
C. rufoolivaceus	3	11		(4.5–) 5.0–6.0	
Hebeloma sarcophyllum	1	15		(4.5–) 5.0–6.0	
Hygrophorus leucophaeus	6	30		(4.5–) 5.0–6.0	6.0
H. penarius		12		5.3–6.0	
Inocybe corydalina		13		5.0–6.0	
I. geophila	5	39		(4.5–) 5.0–6.5	5.7
I. jurana		11		5.3–6.5	6.5
I. pyriodora		21		5.5–6.5	6.3
Lactarius azonites	2	22		(4.5–) 5.0–6.3	
L. circellatus	8	47		(4.5–) 5.0–6.5	5.6, 5.9
Leucopaxillus giganteus		9		5.0–6.5	5.1, 5.3, 5.3, 6.2
Lycoperdon echinatum	1	13		(4.5–) 5.0–6.5	
Mycena pelianthina	2	18		(4.5–) 5.0–6.5	5.8
Oudemansiella platyphylla	4	15		(4.5–) 5.0–6.3	
Pholiota lenta	2	21		(4.5–) 5.0–6.3	
Rhodophyllus rhodopolius	2	23		(4.5–) 5.0–6.5	5.1, 5.3
R. sinuosus	2	12		(4.5–) 5.0–6.0	
Russula laeta	1	8		(4.5–) 5.0–6.0	6.0
R. lilacea	2	10		(4.5–) 5.0–6.0	
R. ochroleuca		10		5.0–6.0	
R. pectinatoides	6	33		(4.5–) 5.0–6.3	5.2, 5.4, 5.5
R. persicina		7		(4.5–) 5.0–6.0	
R. rutila	1	14		(4.5–) 5.0–6.5	5.4
R. sororia	1	10		5.5–6.5	5.6, 5.7
R. vinosopurpurea	2	11		(4.5–) 5.0–6.3	5.2, 5.8, 6.1
Tricholoma orirubens		10		5.0–5.5	6.5
			R: 4		
Agaricus squamuliferus		9	3	5.5–7.2	5.6, 6.0, 7.2
Clitocybe geotropa		10	2	5.8–7.0	6.8
Inocybe patouillardi		15	2	5.5–7.2	7.1, 7.2
Lactarius insulsus		10	2	5.5–7.2	
Macrolepiota rhacodes		17	3	5.3–7.2	5.3
Melanoleuca melaleuca		19	2	5.5–7.2	

Table 5 (continued)

	Occurrence number of stands			Usual pH of the actual	Measured soil pH values
	acido-philic forests	sub-acido-philic forests	neutro-baso-philic forests		
			R: 5		
Agaricus bitorquis		1	13	6.8–8.4	7.4, 7.7, 7.8, 8.0, 8.2, 8.4
A. pseudopratensis var. *niveus*			6	7.0–8.0	
Amanita strobiliformis			13	6.5–8.0	7.0, 7.0, 7.4, 7.7, 7.8, 7.8
Hebeloma edurum			7	6.8–8.2	7.9, 8.0, 8.2
H. subcaespitosum			16	6.8–8.2	7.1, 7.9, 8.1
Inocybe caesariata			27	7.0–8.2	7.7, 7.8, 7.8, 8.2, 8.2
I. godeyi		4	8	6.5–8.2	7.6, 8.0, 8.1
Lactarius mairei		13	9	6.5–7.8	6.8, 6.9, 6.9, 7.1, 7.3, 7.6
Leucocoprinus badhamii		2	5	6.5–7.8	
L. pilatianus		1	6	6.5–7.8	
Morchella conica			5	6.8–8.2	7.9
M. esculenta			23	6.8–7.2	7.0, 7.0, 7.3, 7.4, 7.5, 7.6, 7.9, 8.2
			R: 6A		
Agaricus bresadolianus		2	10	5.5–8.0	
A. haemorrhoidarius	3**	10	3	5.3–8.0	5.3, 5.4, 6.2, 6.5, 7.5, 7.6
Hebeloma crustuliniforme		12	3	5.5–8.0	5.4, 5.5, 5.9, 7.2, 7.8
H. sinapizans		9	3	5.8–8.0	6.1, 6.5, 6.6, 7.0, 7.7
Inocybe fastigiata		24	9	5.3–8.0	6.5, 6.9, 7.3, 7.7
I. lanuginella		4	5	5.5–8.0	
Lactarius acerrimus		4	6	5.3–8.0	5.8, 7.8
L. aspideus var. *flavidus*		10	6	5.3–7.5	7.1, 7.3, 7.5
Lepiota aspera		10	6	5.5–7.5	6.3, 6.9, 7.2, 7.5
Lepista luscina		4	6	5.8–8.2	8.1
Rhodophyllus clypeatus		11	6	5.3–7.8	6.8, 7.8
Xerocomus chrysenteron		35	4	5.0–7.8	5.0, 5.1, 5.8, 6.3, 6.3, 7.4, 7.5, 7.6, 7.8
X. rubellus		15	7	5.5–8.2	6.0
			R: 6B		
Agaricus semotus	7	36		4.5–6.8	5.3, 5.6, 5.8, 6.3, 6.7
Amanita pantherina	19	27	1	4.0–7.0	4.3, 4.6, 5.8, 6.0, 6.8, 7.0
A. phalloides	21	43	1	4.0–7.0	4.3, 4.3, 5.3, 5.7, 5.7, 5.8, 6.0, 6.4, 7.4
Clitocybe gibba	13	39	1	4.5–6.8	
Collybia butyracea	19	32	2	4.5–7.0	
Cortinarius cotoneus	8	7	2	4.2–7.0	4.2, 7.2
C. trivialis	19	30	3	4.0–6.8	4.1, 4.1, 4.2, 4.3, 4.3, 5.3, 5.6, 6.0, 6.8
Hygrophorus eburneus	28	30	1	4.0–6.8	6.3, 6.6
Inocybe descissa	10	20	1	4.5–6.8	
Laccaria laccata	38	38	1	4.0–6.8	5.8, 6.3
Leucocoprinus bulbiger	10	14	3	4.2–7.0	7.0
Russula foetens	40	35	3	4.0–6.8	4.0, 5.4, 6.3, 6.3, 6.3, 6.5, 6.6
Tricholoma saponaceum	36	25	2	4.0–6.8	6.8

Table 5 (continued)

	Occurrence number of stands			Usual pH of the actual community type	Measured soil pH values
	acido-philic forests	sub-acido-philic forests	neutro-baso-philic forests		
			R: 6C		
Boletus luridus	4	19	8	4.2–7.8	6.4, 7.0, 7.2, 7.3, 7.5, 7.6, 7.8
Clitocybe inornata	3	19	2	4.5–7.6	5.3, 5.3, 7.3
Coprinus picaceus	1	5	1	4.5–7.6	5.6, 7.6
Cortinarius infractus	10	27	3	4.2–7.6	4.2, 5.4, 7.2, 7.3, 7.6
Gyroporus castaneus	3	12	3	4.2–8.2	5.1, 6.0, 6.5, 6.5, 7.5, 7.6, 7.9, 8.2, 8.2, 8.2
Lactarius controversus	2	6	8	4.8–7.8	
L. ichoratus	2	10	3	4.5–7.8	5.8, 6.2, 7.3, 7.8, 7.8
Lepiota clypeolaria	5	22	2	4.5–7.6	
L. cristata	2	10	5	4.5–8.2	8.0
Lycoperdon molle	21	21	3	4.2–7.6	4.5, 7.4
L. perlatum	17	38	4	4.2–7.6	4.2, 4.4, 5.0, 5.6, 5.6, 6.6, 7.2
Macrolepiota procera	16	25	6	4.2–7.6	4.7, 4.8, 5.3, 5.7, 5.9, 6.0, 7.1, 7.6
Marasmius wynnei	2	21	5	4.5–8.2	
Mycena pura et varietates	26	52	8	4.5–7.6	5.5, 6.0, 6.8
Paxillus involutus	8	22	7	4.0–7.6	3.6, 7.2
Phallus impudicus	1	12	2	4.0–7.6	3.8, 5.0, 5.5, 7.3
Rhodophyllus nidorosus	8	22	4	4.5–7.6	5.8, 6.5, 7.1
Russula decipiens	2	4	5	4.5–7.6	5.8, 6.3, 6.6, 7.2, 7.5
R. luteotacta	8	24	7	4.5–8.2	6.1, 7.6
R. maculata	7	11	1	4.2–7.6	5.7, 7.7
Tricholoma album	4	15	5	4.0–7.6	4.0, 4.8, 6.2, 7.3
T. scalpturatum	6	22	17	4.5–8.2	7.0, 7.8, 7.8, 7.9, 8.1

* Growing on acidified plots of subacidophilous forests

** Growing in leaf-heaps heaped up in pits, where the acidic rock-bed hardly had an effect on the reaction of the leaf-heap

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THE MICROELEMENT CONTENT OF SOME SUBMERGED AND FLOATING AQUATIC PLANTS

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The most common submerged and floating aquatic plants in lake Balaton are capable of accumulating rare elements (microelements) which otherwise can be detected only in small quantities in the water or the sediment of the lake. The concentration of microelements in these plants is $10–10^6$ times higher than in the environment. The species analyzed for microelements are: *Ceratophyllum demersum*, *Hydrocharis morsus-ranae*, *Lemna trisulca*, *Myriophyllum spicatum*, *Potamogeton pectinatus*, *P. perfoliatus* and *Stratiotes aloides*. A filamentous alga species, *Cladophora glomerata*, is also included in the study. Several microelements, such as Bi, Dy, Eu, Sm, Nd, Ag and Sc were detected only in plants. The concentration of each element proved to be a function of the geochemical environment and, in case of Pb, Zn, Cu and As, that of environmental pollution.

Introduction

The elements in the water of lakes primarily come from the geochemical environment by dissolution from the sediment. Another significant source is environment pollution. The concentration of elements determines water usability and influences the organisms and their communities. A relatively high heavy-metal concentration may prevent self-purification processes. The elements to be found in lakes can be detected in the water, sediment, plants and animals.

The advantage of studying plants lies in the fact that aquatic herbs are capable of accumulating even those elements in great quantities that are present only at low concentration in the environment (e.g., 0.02 μg/l in water).

Sampling and methods

Elemental concentrations were determined in the most common floating and submerged aquatic herbs and a filamentous alga of Lake Balaton. These are listed below along with sampling localities given in brackets:
Ceratophyllum submersum (Balatonudvari, Balatonalmádi)
Hydrocharis morsus-ranae (Csopak, Balatonkenese)
Lemna trisulca (Balatonalmádi)
Myriophyllum spicatum (Szigliget, Badacsony)
Potamogeton pectinatus (Csopak)
P. perfoliatus (Balatonberény, Tihany, Balatonfüred, Csopak, Balatonfűzfő)
Cladophora glomerata (Balatonszárszó, Tihany, Balatonfüred).

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Water samples were taken from the zones of submerged and floating plants in front of reed stands and from the middle of lake Balaton at localities given below. (Sewage inflows are indicated by a cross.)

Balatonmáriafürdő: at the Western collecting canal +, Keszthely: at the mouth of the Csókakő stream +, Balatongyörök, Szigliget, Badacsony, Badacsonytomaj, Balatonudvari, Tihany: Bozsai-Bay, Balatonfüred: on the shore at the sewage purificator +, Csopak: Kerekedi-Bay, Balatonalmádi, Balatonkenese, Keszthely: in the middle of Lake Balaton, Siófok: in the middle of Lake Balaton.

Each water sample was dried in a teflon vessel, under an infra-red lamp. The dry remainder was exsiccated further at 105 °C, and then, after cooling down, it was weighed. The desiccated sample was burnt to ashes by heating at 500 °C for 3 hours. The whole quantity of ashes was subjected to analysis after homogenization with graphyte at a ratio of 1 : 1.

The plant samples were washed with distilled water, dried and ground.

The elemental concentrations were determined by spark-source mass spectrometer in the ashes after heating at 500 °C.

The water and plant samples were analyzed at the laboratory of the Central Research Institute for Physics of the Hungarian Academy of Sciences.

Spectrometry, just like other instrumental analytical methods, has the disadvantage that 3–4 elements cannot be measured precisely. Such element is, for example, Zn. If a given compound of Zn and some anion has a relatively low boiling point, or low sublimation temperature, even the whole quantity of this may leave the sample after heating at 500 °C. Therefore, under certain circumstances, the Zn concentrations measured are lower than the actual concentrations. This is most likely the case with the low Zn concentrations found in the water of Lake Balaton. Furthermore, the concentration of Zn and Cu may fluctuate depending on the fungicide impact of the lake. The fungicides widely used in vineyards may be gradually dissolved as time elapses, or deposited to the bottom in form of complex compounds.

Results

Microelement content of the water of Lake Balaton

The analysis detected the following microelements in the water of Lake Balaton: U, Pb, Ho, Gd, Pr, Ce, La, Ba, Cs, Sb, Sn, Mo, Nb, Zr, Y, Sr, Rb, Br, Se, As, Ga, Zn, Cu, Ni Co, Fe, Mn, Cr, V, Ti, Al, F, B. Toxic elements are underlined according to WOOD (1974) and WILSON (1979).

One source of the elements is the variable geochemical environment of the watershed area of Lake Balaton and its surroudings. On the southern shore sand, loess, and fen-peat are common whereas the northern shore is characterized by limestone, dolomite, basalt and sandstone. Elements get into the lake also with precipitation and different streams.

The highest number of microelements was detected in the water samples from the Badacsony area (30 elements, Table 1). A relatively large quantity of Ga was found to be characteristic of the Keszthely-Bay and the Balatonalmádi–Balatonkenese area. A significant concentration of Ga (160 μg/l) was indicated at Balatonmáriafürdő, in front of the mouth of the Western collecting canal (Table 2). High concentrations of bromine were found in the water samples from the Badacsonytomaj–Balatonudvari area. Relatively large quantities of arsenic were determined in the samples from Keszthely and Balatonalmádi–Balatonkenese. High concentrations of titanium were indicated in the water samples from Keszthely and Tihany.

Element content of plants, the concentration-factor of elements

The macroelement content of some floating and submerged aquatic herbs in Lake Balaton is known from reports by KOVÁCS (1978), KOVÁCS and TÓTH (1979) and TEHERANI et al. (1981). Concentrations of heavy metals in animal species have been studied by SALÁNKI

Table 1

Microelement content of the water of Lake Balaton (in μg/l)

	1	2	3	4	5
U	0.3	—	1.5	0.15	—
Pb	—*	2.1	1.6	—	—
Ho	—	—	—	0.072	—
Gd	10.00	0.76	6.7	0.33	2.7
Pr	—	—	0.11	0.41	—
Ce	—	—	0.44	—	—
La	0.091	0.56	0.43	1.5	—
Ba	10.0	15.0	18.0	1.7	4.2
Cs	—	—	0.021	—	—
Sb	0.37	0.42	0.88	0.46	0.076
Sn	0.64	—	—	—	—
Mo	2.1	0.60	3.7	0.65	3.2
Nb	—	—	—	—	—
Zr	0.92	—	1.1	—	0.47
Y	—	0.089	0.18	0.039	0.12
Sr	190.0	64.0	220.0	12.0	86.0
Rb	0.41	0.094	0.49	0.13	0.42
Br	8.6	6.6	25	18	8.4
Se	0.21	0.43	0.25	0.070	0.58
As	0.98	2	4.7	0.82	0.81
Ga	20	4.6	7.1	2.5	4.1
Zn	0.29	0.21	0.24	0.43	0.28
Cu	0.68	0.36	0.38	1.0	0.49
Ni	0.59	0.90	0.93	0.33	0.80
Co	0.077	0.16	0.092	0.052	0.32
Fe	160	120	1,900	2.7	23,000
Mn	5.8	4.4	10	0.36	59
Cr	2.2	1.2	3.9	0.27	9.6
V	1.3	1.4	3.2	0.11	3.7
Ti	3	2.3	5.1	0.14	6.2
Al	71	32	250	0.089	44
F	50	15	59	42	170
B	18	14	14	50	18

1 = Balatongyörök-Szépkilátó; 2 = Szigliget; 3 = Badacsony–Badacsonytomaj; 4 = Balatonudvari; 5 = Tihany: Bozsai-Bay.

* Elements not present

Table 2

Microelement content of the water of Lake Balaton (in μg/l)

	1	2	3
U	0.33	—	0.58
Pb	—	2.3	—
Ho	0.11	—	—
Gd	3	13	—
Pr	0.098	—	—
Ce	0.22	0.61	—
La	0.13	0.54	—
Ba	1.6	9.6	14
Cs	0.025	—	—
Sb	0.39	0.61	1
Sn	—	—	—
Mo	1.7	1.7	2.9
Nb	—	—	—
Zr	—	1	0.42
Y	0.12	—	—
Sr	13	93	77
Rb	0.33	0.34	0.11
Br	11	9.5	7.9
Se	0.33	0.23	0.39
As	3	2.2	1.8
Ga	160	13	2.8
Zn	0.55	0.65	0.95
Cu	0.63	0.71	0.44
Ni	0.62	0.87	0.54
Co	0.055	0.34	0.57
Fe	17	180	8.4
Mn	1.1	4.8	1.1
Cr	0.12	0.72	0.4
V	0.36	0.85	0.49
Ti	0.80	4.5	1.4
Al	0.75	940	20
F	5.3	5.5	9.2
B	32	40	17

1 = Balatonmáriafürdő: at the mouth of the Western collecting canal; 2 = Keszthely: at the mouth of the Csókakő stream; 3 = Balatonfüred: at the mouth of the sewage purificator

Table 3

The microelement of the dry matter of Ceratophyllum submersum (in ppm)

	1	2		1	2
Bi	—	0.41	Br	+	20.62
Pb	52.35	51.54	As	+	20.62
Nd	1.22	14.43	Ga	1.74	5.18
Pr	0.17	4.12	Zn	*	14.43
Ce	1.74	20.62	Cu	17.45	5.15
La	0.52	41.24	Ni	87.26	30.93
Ba	**	**	Co	5.23	30.93
Cs	0.17	6.19	Fe	***	***
I	15.70	103.09	Mn	**	**
Sb	82.02	1.03	Cr	122.16	16.49
Sn	0.35	2.06	V	10.47	30.93
Mo	5.23	5.15	Ti	87.26	123.71
Nb	0.17	2.47	Al	***	***
Zr	1.74	10.34	Sc	—	1.24
Y	0.35	5.15	F	0.70	1.03
Sr	**	**	B	29.67	12.37
Rb	—	**			

1 = Balatonalmádi; 2 = Balatonudvari
Explanations for symbols (also used in Tables 5–11):
— the sample does not contain the element in question
+ ash-matter contains the element in question but its concentration cannot be determined due to the superposition of spectroscopic lines of other elements
* 0.1–0.2% of the total weight of ashes, estimated value
** 0.2–1.0% of the total weight of ashes, estimated value
*** over 1.0% of the total weight of ashes, estimated value

et al. (1981, 1982). The microelement content of the most common species will be discussed below.

Ceratophyllum submersum (Table 3)

A submerged and rooting plant of the littoral zone where water is rich in nutrients. Having fringed-pinnatifid leaves, this plant has a large absorption surface. Of the detectable 33 elements it contains Pb, Ni, Cr, Br, As, V, and Ti in relatively large quantities. The Pr, Ce, La, Cs, I, Zr, Y, Ga and Co content of the samples from Balatonudvari results from the special geochemical enviroment of this area. The high Sb and Cu content of the plants from Balatonalmádi suggests the existence of industrial pollution. The concentration-factor of the elements* is between 10 and 10^5 (Table 4), the most intensively accumulated elements being Cs, Sb, Y, Ni, Co, Cr, V and Ti.

* Concentration-factor $= \frac{\text{element content in the plant, ppm/dry matter}}{\text{element content in the water, } \mu\text{g/ml}}$ (cf. Bowen 1956, Morris and Bale 1975, Foster 1976).

Table 4

The concentration-factor of each microelement in some aquatic plants

	1	2	3	4	5	6	7
Pb	10^4	10^3–10^4	10^3	10^3–10^4	10^2–10^3	10^2–10^3	10^3
Pr	10^2–10^4	10^2	10^3	10^3–10^4	10^2–10^3	10^2–10^3	10^2–10^3
Ce	10^3–10^4	10^2–10^3	10^3	10^4	10^3	10^3–10^4	10^2–10^4
La	10^3–10^4	10^3	10^3	10^3–10^4	10^3	10^2–10^3	10^2–10^3
Cs	10^3–10^5	10^3	—	10^4–10^5	10^4	10^4	10^3–10^4
Sb	10^3–10^5	10^3–10^4	10^5	10^2	10^3	10^2–10^3	10^3
Sn	10^3	10^3–10^4	10^4	10^3	10^2	10^2–10^3	10^2–10^3
Mo	10^3	10^3	10^2	10^2–10^4	10^2–10^3	10^2–10^4	-10^2–10^3
Nb	10^2–10^3	10^3	10^3	10^3–10^4	10^3	10^2–10^3	10^2–10^3
Zr	10^3	10^2–10^3	10^2	10^3–10^4	10^2–10^3	10^2–10^3	10
Y	10^3–10^5	10^2–10^3	10^3	10^4	10^2–10^3	10^3	10^2–10^3
Br	10^3	10^3	—	10^3	10^3	10^2–10^3	10^3
As	10^4	10^4	—	10^2–10^3	10^2	10^2	10^3
Ga	10–10^3	10–10^3	10	10^2–10^3	10^2	10^2	10–10^3
Zn	10^4	10^5	10^4	10^6	10^4–10^5	10^4–10^5	10^4–10^5
Cu	10^3–10^4	10^4	10^4	10^5	10^3–10^4	10^4	10^4
Ni	10^4–10^5	10^4	10^3	10^4	10^3–10^4	10^4	10^3–10^4
Co	10^3–10^5	10^3–10^4	10^2	10^4–10^5	10^3–10^4	10^3–10^4	10^2–10^5
Cr	10^4–10^5	10^2–10^3	10^3	10^3–10^4	10^4	10^3–10^4	10^3
V	10^3–10^5	10^3	10^3	10^4	10^3	10^3–10^4	10^2–10^4
Ti	10^4–10^5	10^4	10^4	10^5	10^4	10^4–10^5	10^4–10^5

1. *Ceratophyllum submersum*
2. *Hydrocharis morsus ranae*
3. *Lemna trisulca*
4. *Myriophyllum spicatum*
5. *Potamogeton pectinatus*
6. *Potamogeton perfoliatus*
7. *Stratiotes aloides*

Hydrocharis morsus ranae (Table 5)

It is a floating plant characteristic of the reed stands in Lake Balaton. Thirty-one microelements were detected, Zn, Ni, Ti, Sc and B in large quantities. As a result of an industrial sewage load at Balatonkenese, frog-bit can take up Sb, As, Zn and Co in large quantities. Zn has the highest concentration-factor in this plant (Table 4).

Lemna trisulca (Table 6)

Twenty-six microelements were detected in this submerged species found commonly among reeds. It contained Sb, Sn, Cu, Ti and B in large quantities. It can take up Zn from water up to a concentration-factor of 10^5 (cf. Table 4).

Table 5

The microelement content of the dry matter of Hydrocharis morsus ranae (in ppm)

	Csopak	Balatonkenese		Csopak	Balatonkenese
Pb	6.74	2.21	Rb	—	*
Nd	2.02	1.50	Br	—	85.65
Pr	—	0.21	As	—	107.07
Ce	0.22	1.28	Ga	5.62	2.14
La	—	0.43	Zn	80.90	321.20
Ba	119.10	**	Cu	13.48	12.85
Cs	—	0.64	Ni	33.71	32.12
I	4.49	32.12	Co	1.80	32.12
Sb	13.48	1.07	Fe	**	***
Sn	19.95	1.07	Mn	**	**
Ag	6.74	—	Cr	1.80	0.86
Mo	5.62	5.35	V	1.57	6.42
Nb	—	0.26	Ti	51.68	53.53
Zr	0.22	2.57	Sc	157.30	0.06
Y	0.22	0.53	F	0.67	0.53
Sr	**	**	B	38.20	64.24

Table 6

The microelement content of dry-matter of Lemna trisulca (in ppm)

	Balatonalmádi		Balatonalmádi
Pb	22.17	Ga	0.88
Pr	0.44	Zn	73.17
Ce	2.22	Cu	48.78
La	0.88	Ni	6.65
Ba	**	Co	0.88
I	0.44	Fe	**
Sb	117.51	Mn	**
Sn	19.95	Cr	3.32
Mo	2.22	V	3.22
Nb	2.22	Ti	119.73
Zr	0.88	Sc	**
Y	0.44	F	2.22
Sr	**	B	190.69

Table 7

Microelement content of the dry-matter of Myriophyllum spicatum (in ppm)

	Szigliget	Badacsony		Szigliget	Badacsony
Bi	0.27	—	Rb	*	*
Pb	9.82	21.83	Br	39.29	87.34
Nd	13.57	30.57	As	19.65	0.87
Pr	0.79	4.37	Ga	2.36	10.92
Ce	7.86	17.47	Zn	294.69	349.34
La	1.96	8.73	Cu	49.12	56.77
Ba	**	**	Ni	11.79	65.50
Cs	1.96	13.10	Fe	***	***
I	15.72	13.10	Mn	**	**
Sb	0.39	0.65	Co	15.72	17.47
Sn	0.98	2.18	Cr	7.86	65.50
Mo	6.88	2.18	V	29.47	65.50
Nb	1.18	2.62	Ti	491.16	2620.10
Zr	9.82	21.83	Sc	0.24	2.62
Y	2.36	5.24	F	1.09	13.10
Sr	**	**			

Myriophyllum spicatum (Table 7)

It is one of the most frequent submerged aquatic plants in Lake Balaton, which can be found both in the foreground of the reed stands and in the open water. It contains microelements in large quantities and its microelement composition is similar to that of *Ceratophyllum submersum*. High concentrations of Pb, Nd, I, Zr, Y and V are characteristic for this species. The Zn and Cu accumulation in the Badacsony-Szigliget samples allows for the conclusion that the Zn and Cu containing fungicides extensively used in vineyards are washed into the lake.

In the Badacsony area, Pr, Ce, La, Cs, Ga and Cr can be detected in relatively large quantities. Water-milfoil can take up Zn at a concentration-factor of 10^6, whereas this factor is 10^5 for Cs, Co and Ti (cf. Table 4).

Potamogeton pectinatus (Table 8)

This pondweed species is rooted to the bottom. Common both in the open water of Lake Balaton and in the foreground of the reed stands. With the fringed and submerged leaves it is able to take up large quantities of elements directly from the water (cf. ABO-RADY 1980, HANNERZ 1968). It accumulates large quantities of Pb, Br, Ni, Ti, B, Zn and Cu. It takes up Zn from the geochemical environment in the largest quantity which corresponds to a concentration-factor of 10^5 (cf. Table 4).

Table 8

Microelement content of the dry-matter of Potamogeton pectinatus (in ppm)

	Csopak: Kerekedi öböl			Csopak: Kerekedi öböl	
Pb	1.49	15.97	Br	+	31.95
Nd	0.60	2.40	As	+	0.33
Pr	0.15	0.32	Ga	1.49	0.02
Ce	0.60	1.60	Zn	11.96	127.79
La	4.24	0.64	Cu	2.99	20.77
Ba	**	*	Ni	8.97	23.96
Cs	0.30	1.60	Co	1.19	12.78
I	—	0.32	Fe	**	**
Sb	1.49	1.28	Mn	*	**
Sn	0.30	0.48	Cr	5.23	6.39
Ag	—	—	V	4.48	4.79
Mo	3.73	1.60	Ti	80.72	95.85
Nb	1.49	0.40	Sc	—	0.19
Zr	0.60	1.92	Al	**	—
Y	0.15	0.64	F	1.49	0.05
Sr	**	**	B	52.31	958.5
Rb	**	**			

Potamogeton perfoliatus (Table 9)

It is the third most frequent rooted pondweed species and is found both in the littoral zone and in the open water. 33 microelements were detected in this herb. The element content of the leaves is two or three times larger than that of the stem. High concentrations of lead, zinc and titanium were indicated in the leaves whereas a high boron-content is characteristic of the stems. Relatively large quantities of I, Mo, Zr, Ga, Cu, Ni and Co are also characteristic of this species (cf. Table 4).

Stratiotes aloides (Table 10)

The stands of this rooted and mostly floating herb, which used to be distributed extensively on the northern shore of Lake Balaton up to the middle of the 70's, have been decreasing in area for years. Submerged individuals are also frequent in the summer. High concentrations of Sb, Y, Zn, Cu, Ni, Co and Ti are also characteristic of the submerged individuals. The concentration-factors of Y, Zn, Co and Ti can be as high as 10^5 (cf. Table 4).

Cladophora glomerata (Table 11)

The majority of microelements, namely 38 of them, were detected in this alga species. The presence of the lantanids (La, Ce, Pr, Nd, Sm, Eu, Gd, Dy, Ho) is characteristic of the samples from Balatonszárszó. *Cladophora glomerata* is able to take up large quantities of the following elements: Pb, I, Zr, Br, Zn, Cu, Ni, Cr, V and B (Table 12).

Table 9

Microelement content in the dry-matter of the organs of Potamogeton perfoliatus (in ppm)

	1		2	3		4	
	L	S		L	S	L	S
Bi	—	—	0.34	—	—	—	—
Pb	5.48	0.81	33.97	6.66	4.29	13.87	2.19
Nd	2.19	0.81	4.24	2.66	2.40	4.85	1.02
Pr	0.31	0.16	0.85	0.53	0.34	0.55	0.15
Ce	2.19	1.62	9.55	2.66	1.71	5.55	0.58
La	1.25	0.65	4.24	1.33	0.69	1.39	0.29
Ba	**	**	**	**	**	**	*
Cs	0.47	0.48	0.72	1.33	1.71	1.39	0.44
I	23.47	24.27	42.46	4.00	25.73	11.09	4.37
Sb	0.47	0.24	**	0.26	0.86	0.42	0.73
Sn	0.39	0.40	6.37	0.40	0.86	0.69	0.29
Ag	—	—	12.74	—	—	—	—
Mo	0.78	0.81	12.74	1.33	1.71	31.21	0.73
Nb	0.39	1.94	3.18	0.33	0.43	0.83	0.17
Zr	3.91	1.94	10.61	2.00	2.06	3.47	0.73
Y	0.94	0.97	5.31	0.80	0.69	0.83	0.36
Sr	**	**	***	**	**	**	**
Rb	*	**	+	*	**	**	*
Br	15.65	64.72	+	5.33	85.76	27.74	58.31
As	0.78	0.81	+	1.33	8.58	0.69	0.73
Ga	1.88	1.94	10.61	1.33	1.71	1.39	1.46
Zn	49.95	24.27	**	106.66	51.46	208.04	21.87
Cu	39.12	21.03	63.69	17.33	34.30	34.67	18.95
Ni	31.30	4.85	33.97	20.00	10.29	20.80	36.44
Co	7.82	2.43	36.09	5.33	2.57	20.80	2.19
Fe	***	***	***	***	***	***	**
Mn	**	**	**	**	**	**	**
Cr	12.52	2.43	42.46	5.33	6.86	11.09	2.19
V	23.47	4.85	31.85	13.33	5.14	20.80	2.19
Ti	391.26	194.17	**	266.66	171.53	277.39	36.44
Sc	0.19	0.10	—	0.40	0.21	0.42	0.09
F	0.19	0.05	12.74	0.06	0.09	0.04	0.04
B	0.47	0.97	42.46	13.33	17.15	41.61	43.73

1 = Balatonberény; 2 = Tihany: Bozsai-Bay; 3 = Balatonfüred: at the sewage purificator; 4 = Csopak: Kerekedi-Bay
L = leaf; S = stem

Table 10

Microelement content of the dry-matter of Stratiotes aloides (in ppm)

	1	2	3	4
Pb	6.05	2.66	4.94	2.33
Nd	1.69	—	—	1.16
Pr	0.48	—	—	0.23
Ce	4.84	0.26	0.33	0.93
La	2.18	0.26	0.16	0.46
Ba	*	69.33	*	—
Cs	0.72	—	0.16	0.70
I	19.37	2.66	3.29	18.60
Sb	1.21	—	0.99	0.70
Sn	2.42	0.26	1.65	0.58
Ag	—	—	1.33	—
Mo	6.05	2.66	4.12	2.33
Nb	0.48	0.53	0.33	0.19
Zr	0.97	—	0.33	1.16
Y	1.45	—	0.16	27.91
Sr	**	80.00	**	**
Rb	—	—	—	*
Br	+	+	—	23.26
As	+	+	—	2.33
Ga	4.84	2.66	0.82	1.16
Zn	79.90	24.00	57.66	69.77
Cu	14.53	16.00	41.18	16.28
Ni	33.90	4.00	4.94	23.26
Co	9.68	1.06	0.33	18.60
Fe	**	***	**	—
Mn	**	*	*	—
Cr	3.62	5.33	2.47	1.86
V	7.26	1.06	5.76	3.49
Ti	*	61.33	98.84	139.53
Sc	—	—	—	0.07
Al	***	93.33	*	—
F	6.05	2.66	0.82	0.12
B	41.16	1.06	28.00	2.97

1 = Csopak (under water); 2 = Badacsonytomaj (above water); 3 = Balatonfűzfő (under water); 4 = Balatonudvari (under water)

Table 11

Microelement content of the dry-matter of Cladophora glomerata (in ppm)

	1	2	3		1	2	3
Pb	8	14.33	33.48	Y	5	1.72	5.58
Ho	0.2	—	—	Sr	80	**	**
Dy	1.4	—	—	Rb	60	—	*
Gd	1	—	—	Br	2.5	*	44.64
Eu	0.5	—	—	As	6	*	1.12
Sm	2.5	—	—	Ga	6	5.73	3.35
Nd	8	2.00	7.81	Zn	100	94.57	178.57
Pr	1.4	0.28	0.89	Cu	35	28.66	55.80
Ce	12	1.14	8.93	Ni	80	*	13.39
La	5	0.57	2.23	Co	8	4.29	8.93
Ba	70	**	**	Fe	800	***	**
Cs	5	0.28	0.45	Mn	50	*	*
I	0.5	8.59	17.86	Cr	40	2.29	17.86
Sb	0.4	1.43	1.12	V	*	17.19	33.48
Sn	1.4	12.89	5.58	Ti	**	154.76	223.21
Ag	0.3	—	—	Sc	—	—	0.67
Mo	0.6	2.86	2.23	F	15	7.16	0.27
Nb	1.4	5.73	1.34	B	80	246.47	33.48
Zr	7	2.86	26.78				

1 = Balatonszárszó; 2 = Tihany: Bozsai-Bay; 3 = Balatonfüred: at the sewage purificator

Table 12

The concentration-factors of some microelements in Cladophora glomerata

Pb	10^3	As	10^2
Pr	10^3	Ga	10^3
Ce	10^3–10^4	Zn	10^5
La	10^3	Cu	10^4–10^5
Cs	10^3–10^4	Ni	10^4
Sb	10^3–10^4	Co	10^4
Sn	10^4	Cr	10^2–10^4
Mo	10^2	V	10^3–10^4
Nb	10^4	Ti	10^4–10^5
Zr	10^3–10^4	F	10
Y	10^4	B	10^3–10^4
Br	10^3		

Summary

Our results suggest that microelements are accumulated in extremely variable quantities by the floating and submerged plants and alga species studied. Whereas the macroelement content is generally a specific feature of plants, the uptake of microelements (inc. heavy metals) depends on environmental conditions (cf. DIETZ 1972). The aquatic-plants, as accumulative indicators, are suitable for characterizing the geochemical environment and detecting various elements in the sewage load.

Uranium in the water of the lake was not detected in the plants. Several elements, such as Bi, Dy, Eu, Sm, Nd, I, Ag and Sc were not found in the water but occurred in the plant samples.

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FORCED ASSOCIATION BETWEEN NITROGEN-FIXING BACTERIA AND GREEN ALGA*

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The associative culture of the green alga *Chlamydomonas reinhardii* and either of two nitrogen-fixing *Azotobacter* species (*A. vinelandii* and *A. chroococcum*) was produced and grown on nitrogen and carbon deficient minimal medium. Nitrogenase activity and photosynthetic O_2 evolution was measured in the cultures. The results show a good working interaction between bacterial and algal cells.

Scanning electron micrographs reveal that bacterial cells are localized close to the surface of algal cells.

In recent years many attempts have been made to enhance biological nitrogen fixation with respect to its contribution to the nitrogen nutrition of higher plants. One considerable approach to this goal may be the extension of nitrogen-fixing symbioses to various non-leguminous species. On the basis of some naturally occurring associations between higher plants and free-living N_2-fixing bacteria (DÖBEREINER et al. 1972, BURNS and HARDY 1975 STEWART et al. 1979), it seems feasible to force these bacteria into symbioses with plant tissues. Hitherto nearly all of these forced associations aimed only at the nitrogen supply of the eukaryote partner and the energy requirements of nitrogen-fixation were met by carbohydrates added to the medium (CARLSON and CHALEFF 1974, BUTENKO et al. 1982).

The question arises whether autotrophic growth can be maintained in a symbiotic system containing a so-called non-symbiotic nitrogen-fixing bacterium and a non-leguminous photosynthetizing organism. In the work presented here cells of unicellular green alga, *Chlamydomonas reinhardii* were forced into association with cells of strictly aerobic nitrogen-fixing *Azotobacter* species. The fate and functioning of this association was observed for several months, and the level of contact was studied in the cultures.

Wild type strains of *Chlamydomonas reinhardii*, *Azotobacter vinelandii*, *A. chroococcum*, *A. beijerinckii*, *Azorhizophilus paspali*, *Azomonas agilis* and *Azomonotrichon macrocytogenes* were used. Nitrogenase activity was measured by the acetylene reduction assay, ethylene was determined by gas chromatography (BURRIS 1972). The nitrogenase activity of the N_2-fixing bacteria was compared (Table 1) and two of the most effective ones (*Azotobacter vinelandii* and *A. chroococcum*) were used in the associative cultures. These cultures were produced by mixing *Azotobacter* and *Chlamydomonas* cells on agar plates lacking all kinds of combined nitrogen and utilizable carbon sources. The cultures were grown under a 12 h light (3000 lux) and 12 h dark regime. Photosynthetic O_2 evolution was measured in liquid culture by using an oxygen-sensitive electrode. Cell density was approximately 10^6 cells/ml while temperature and light intensity were 25 °C and 20 000 lux, respectively. Chlorophyll content of algal cells was extracted in 80% acetone and estimated from the absorbance data measured at 644 and

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Table 1

Nitrogenase activity in a few aerobic N_2 fixing bacterium

Species	Ethylene, nmol/10^8 cells/h
Azotobacter vinelandii	1.39
A. chroococcum	1.12
A. beijerinckii	0.95
Azorhizophilus paspali	1.02
Azomonas agilis	0.83
Azomonotrichon macrocytogenes	0.75

662 nm by the formula of AVRON (1960). For scanning electron microscopy cells were fixed in 2.5% glutaraldehyde for 1 h. After washing samples were dehydrated in ethanol series and dried then coated with gold. Examination was made with a Jeol 50/A scanning electron microscope at 15 kV. Glutamine synthetase enzymes were separated by polyacrylamide gel electrophoresis and visualized by the method of NAGY et al. (1983).

The associative cultures were showing slow but visible growth, the algal cells retained their green colour while control cultures of *Chlamydomonas* on the same minimal medium turned yellow and died within 2 months. Some of these cultures have been living for more than a year by now.

Structural characteristics of settled cultures (having lived for at least four months on minimal medium) were investigated by scanning electron microscopy and by calculating a cell number ratio of bacterial to algal cells.

Scanning electron micrograph (Fig. 1) shows a few bacteria closely connected with each algal cell. The ratio calculated from viable numbers gave on an average 2–3 times more bacterial than algal cells.

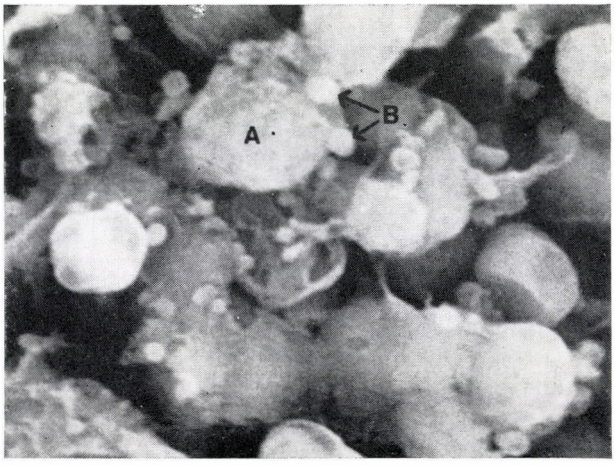

Fig. 1. Scanning electron micrograph of the associative culture of *Chlamydomonas reinhardii* and *Azotobacter vinelandii*. ×6200. A = alga; B = bacterium

Some features relating photosynthetic effectiveness of algal cells in symbiotic cultures were compared with control alga growing on a medium supplied with NH_4Cl (Table 2). The chlorophyll content of cells was close to

Table 2

Chlorophyll content and photosynthetic O_2 evolution of algal cells in associative cultures

Culture	Chlorophyll a+b nmol/10^7 cells	O_2 evolution per	
		10^7 cells, %	chl a+b, %
Chlamydomonas reinhardii (control)	23.4	100	100
C. reinhardii + *A. chroococcum*	22.3	90	95
C. reinhardii + *A. vinelandii*	19.1	88	109

that of the control having appropriate nitrogen supply. Similarly, the rate of photosynthetic O_2-evolution proved to be nearly the same as the value obtained with the control. These data suggest that algal cells in the association are photosynthetically active. Considering the slow growth rate it seems not impossible that carbon compounds are released by algal cells. So far glycolate excretion has been proved for *Chlamydomonas* (TOLBERT 1979) but still we have no data whether *Azotobacter*s can utilize glycolate as a carbon source. However, such excreted materials can be taken up by bacterial cells from the medium.

Nitrogenase activity could be detected in the symbiotic cultures after four months living on the minimal medium. It also shows that bacterial cells do get the energy source for this highly energy requiring reaction.

An increased activity of algal glutamine synthetase was found in symbiotic cultures, showing a greater ability of building ammonium ions into *Chlamydomonas* cells. Nitrogen fixing cultures of *Azotobacter* species are well known to excrete ammonia and other nitrogenous compounds into the medium (NEWTON et al. 1953, KLEINER 1974, KARUBE et al. 1981) providing a way to supply algal cells with sufficient amounts of nitrogen.

Further experiments must be carried out to determine what sort of nitrogenous and carbon compounds do bacterial and algal cells excrete into the medium in addition to the above mentioned ammonia and glycolate. What we can say now is that this associative symbiosis of nitrogen-fixing bacteria and green alga enables the two organisms to grow under conditions not allowing the growth of either partner separately.

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PHYTOCHROME-MEDIATED CONTROL OF PROTEIN SYNTHESIS DURING GERMINATION OF FERN SPORES

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Effects of protein- and RNA-synthesis inhibitors were studied on the [^{3}H] leucine incorporation into the polypeptides in red and far-red illuminated germinating fern spores. Phytochrome-mediated synthesis was proved in production of a 42 000 dalton polypeptide in both of *Pteridium aquilinum* and *Dryopteris filix-mas*. Characteristic phytochrome effect was demonstrated in labelling of 29 000 dalton polypeptide of *P. aquilinum* and 36 000 dalton form of *D. filix-mas*. The red light regulation of 42 000 dalton polypeptide was affected by cycloheximide in both species. The treatment with actinomycin-D appeared to be an effective inhibitor of synthesis of 42 000 dalton form in the spores of *D. filix-mas* only. Light stimulated labelling of 29 000 dalton polypeptide of *P. aquilinum* was inhibited by cycloheximide. The chloramphenicol showed significant effect to prevent the [^{3}H] leucine incorporation into the 36 000 dalton polypeptide in the illuminated spores of *D. filix-mas*.

Introduction

Different types of ferns exhibit varying degrees of sensitivity to morphogenetically active light. Spores of *P. aquilinum*, *Ceratopteris thalictroides* and *Osmunda regalis* are known to be able to develop beyond the first cell division on simple mineral solution even in the absence of light (MILLER 1968) but the majority of fern species cannot germinate in darkness. The germination of fern spores was demonstrated to be stimulated under red light illumination and delayed under blue and far-red light (MOHR 1956). A typical red and far-red reversible reaction was first shown to be involved in the spore germination in the fern *Pteris* (SUGAI and FURUYA 1967). The germination of spores in *Lygodium* is controlled by both phytochrome and a blue light absorbing pigment (SUGAI et al. 1977). Light controlled germination has been reported in *D. filix-mas* (BÜNNING and MOHR 1955). The morphological aspects of germination have been studied and detailed descriptions of developmental events are available (MILLER 1968). Recent research however, has been directed toward understanding the physiological and molecular mechanisms involved in spore germination (RAGHAVAN 1976, 1977).

Phytochrome controlled synthesis of proteins were demonstrated in two fern species in our earlier paper (NAGY et al. 1978). In the present study the characteristics of the phytochrome effect on protein synthesis is studied. Using cycloheximide and chloramphenicol, which are known to selectively inhibit cytoplasmic and organellar protein synthesis respectively, we attempt to determine the location of protein synthesis controlled by active phytochrome. Using actinomycin-D, an inhibitor of mRNA synthesis, we try to analyse the phytochrome effect at the transcriptional level.

Materials and methods

Plant material

The spores of two fern species were collected from an experimental garden. The plants of *Dryopteris filix-mas* were originally transplanted from a natural population near Szőce (Őrség, Western Hungary). The bracken, *Pteridium aquilinum*, was originally collected from a natural population near Pilisszentiván (20 km NW of Budapest, Hungary).

Cultivation methods

50 mg dry weight of spores were sown on the surface of 10 ml sterilized mineral salt medium (Knop solution) in a Petri dish, then placed in complete darkness into a controlled chamber (25 $\pm$ 2 °C). After 48 h incubation in the dark, the spores were treated with the inhibitors and subsequently irradiated. The light treatment consisted either of a 15 min exposure of red light (675 nm) or of two subsequent exposures of 7.5 min of red (675 nm) and 7.5 min of far-red (725 nm) (light stimulated). A Zeutschel M-3 S power supply and Zeiss metall-interference filters were used as red and far-red sources, adjusted to equal energy (0.08 Wm^{-2}). The light treatments were subsequently repeated every 24 h and the experiment was terminated at the 144th h.

Drug treatment and labeling of proteins

2 h before the first light treatment actinomycin-D (the inhibitor of mRNA synthesis) was added to the medium to a final concentration of 0.1 mg/l. Cycloheximide (in 50 mg/l final concentration) and chloramphenicol (in 175 mg/l final concentration) were added 1 h before the exposure to light. Immediately prior to the light treatments 11.1 MBq 4.5-[^{3}H] leucin (0.66 mM leucin) was added to the samples after preincubation with the inhibitors.

Sample preparation for electrophoresis

Spores from one Petri dish were collected and the washed cells were homogenized in 1 ml of 0.01 M sodium phosphate buffer, pH 7.2, containing 1% Sodium dodecylsulphate (SDS) and 1% 2-mercaptoethanol (WEBER et al. 1972). The slurry was boiled for 2 min and centrifuged at 2000 g for 10 min. Solid iodo-acetamide was added to a final concentration of 0.3 M. The samples were subsequently incubated for 1 h at room temperature and then dialyzed for 24 h against 0.01 M sodium phosphate buffer, pH 7.2, which contained 0.1% SDS and 0.1% 2-mercaptoethanol. An aliquot was removed from each sample to determine the amount of radioactivity present. Sample containing 300 γ protein were electrophoresed on SDS-polyacrylamide gels.

Polyacrylamide gels

Polyacrylamide gels were prepared according to the procedure of WEBER et al. (1972) using 0.8% N,N'-diallyltartardiamide (DATD) as the crosslinker. 10% acrylamide gels were used within 12 hours after polymerization. Electrophoresis was carried out according to WEBER et al. (1972).

Preparation of gel slices for scintillation counting

After completion of electrophoresis, the gel was cut into 2 mm slices and 0.5 ml of 2% periodic acid and the gel slice were added to a scintillation vial. After 30 min of oxidation at room temperature, 5 ml of a toluene-Triton-X-100 scintillation solution (30% triton X-100) was added to each vial (ANKER 1970). The quantity of [^{3}H] in each gel slice was determined on a Beckman LS-100 instrument.

Each experiment contained duplicate samples and was repeated three times. The *t* statistic was calculated from the data of 6 gel columns.

Electron microscopy

The young gametophytes of *P. aquilinum* were collected from the Knop solution and fixed in 5% glutaraldehyde (0.07 M K–Na phosphate buffer, pH 7.2) for 24 h at 4 °C. After thorough washing, a postfixation followed in 1% OsO_4 using the same buffer for 2 h at 4 °C.

The gametophytes were dehydrated in ethanol series and propylene oxide, then embedded in Durcupan ACM (Fluka).

The 144 h spores of *D. filix-mas* were treated by the method of BASSEL et al. (1981). The spores were fixed in 3.5% glutaraldehide (0.1 M phosphate buffer, pH 7.2) for 24 h at 4 °C. After three washes in buffer the spores were treated with 1% NaOCl in 0.1 M mannitol for 45 or 90 minutes. After washing the spores were postfixed with 1% OsO_4 in 0.1 M buffer for 1 h, the cells were treated with 1% NaOCl for an additional 30 min followed by fixation with OsO_4 for an additional 30 min. The spores were dehydrated through ethanol series and propylene oxide and embedded in SPURR's (Polysciences) low viscosity epoxy resin (SPURR 1969). The sections were made on a Porter-Blum MT-1 ultramicrotome, stained with uranyl acetate and lead citrate and examined with a Tesla BS 500 electron microscope.

Results

Radioactivity profiles of solubilized proteins

Figure 1. shows the ^3H labelling of polypeptides of germinating spores of *P. aquilinum* (a) and *D. filix-mas* (b) in darkness and after treatment with red and far-red light. The red light (675 nm) stimulated the ^3H leucine incorporation into the 42 kd polypeptide in both of the species. Two additional polypeptides were affected by of the red light, there were the 29 kd type of *P. aquilinum* and the 36 kd form of *D. filix-mas*. The 36 kd polypeptide of

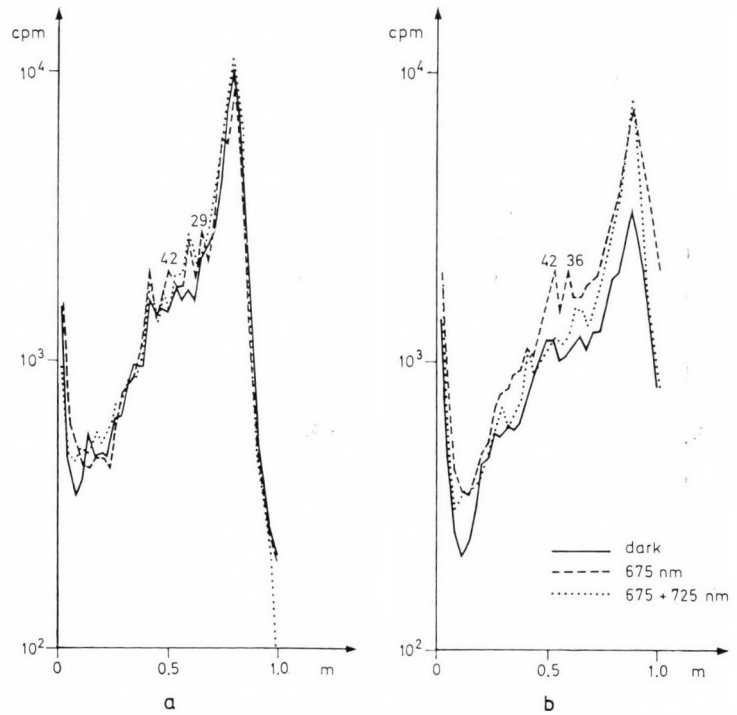

Fig. 1. Radioactivity profile of the polypeptides of 144 h old gametophytes (a: *Pteridium aquilinum*; b: *Dryopteris filix-mas*) in darkness and after illumination with red and far-red light (m = mobility). Significance of *t* (a) 42 kd $P < 0.05$; 29 kd $P < 0.10$; (b) 42 kd $P < 0.02$; 36 kd $P < 0.05$

P. aquilinum was affected by the two types of light treatment. The red light was more effective to increase the ^{3}H leucine incorporation into the polypeptides of *Dryopteris* gametophyte. This was a characteristic difference between the two species.

Effect of inhibitors on light stimulated protein synthesis

Statistical analysis of data obtained in radioactive labelling of three phytochrome stimulated polypeptides after treatment with inhibitors is shown in Tables 1 and 2. Cycloheximide significantly inhibited the red light induced incorporation of ^{3}H leucine into the 42 kd polypeptide in both of *P. aquilinum* and *D. filix-mas*. This effect of cycloheximide can also be observed in Fig. 2. The red light stimulated synthesis of 42 kd polypeptide was prevented in illuminated *Dryopteris* spores by the treatment with actinomycin-D. This drug was effective inhibitor in darkness too (Table 1). None of the other polypeptides were affected by the treatment with actinomycin-D. The labelling of 29 kd polypeptide of *Pteridium* gametophyte was sensitive to the presence of cycloheximide. In darkness the radioactive profiles of control and treated samples were similar, but the cycloheximide effectively prevented the red light stimulated incorporation of ^{3}H leucine into the 29 kd polypeptide (Table 2). Characteristic cycloheximid effect was the intense labelling of low molecular weight polypeptides ($\sim$15 kd) in *Pteridium* gametophyte (Fig. 2a).

The red light regulated synthesis of 36 kd polypeptide of *Dryopteris* spores was significantly inhibited by chloramphenicol (Table 2, Fig. 2b). ^{3}H leucine incorporation in darkness into this polypeptide form was also affected by inhibitors. However, the cycloheximide and the actinomycin-D did not prevent the increase of ^{3}H labelling during the treatment with

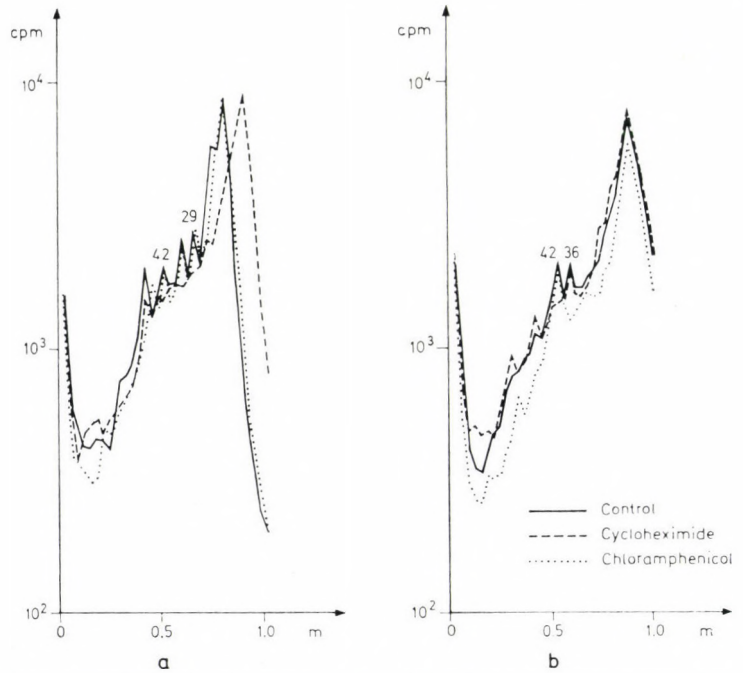

Fig. 2. Effect of inhibitors on incorporation of [^{3}H] leucine into the proteins of red light stimulated fern spores (a: *Pteridium aquilinum*; b: *Dryopteris filix-mas*; m = mobility)

Table 1

Statistical analysis of results obtained in labelling of 42 kd polypeptide during the light and drug treatments*

Treatments	*t* statistics		Significance of *t*	
	P. aquilinum	*D. filix-mas*	*P. aquilinum*	*D. filix-mas*
D				
C–CH	0.61	0.99	>0.60 N.S.	>0.30 N.S.
C–CAP	0.06	1.54	>0.90 N.S.	>0.10 N.S.
C–Act-D	0.29	2.11	>0.80 N.S.	<0.10 S.
CH				
D–R	0.56	0.51	>0.60 N.S.	>0.60 N.S.
D–FR	1.06	0.47	>0.30 N.S.	>0.60 N.S.
R–FR	0.60	0.84	>0.60 N.S.	>0.40 N.S.
CAP				
D–R	2.48	2.58	<0.05 S.	<0.05 S.
D–FR	0.36	0.22	>0.70 N.S.	>0.80 N.S.
R–FR	2.63	2.29	<0.05 S.	<0.05 S.
Act-D				
D–R	1.97	1.82	<0.10 S.	>0.10 N.S.
D–FR	1.27	1.25	>0.20 N.S.	>0.20 N.S.
R–FR	3.71	0.75	<0.01 S.	>0.40 N.S.

* 42 ± 2.1 kd; S = significant; N.S. = non-significant; C = control; CH = cycloheximide; CAP = chloramphenicol; Act-D = actinomycin-D; D = dark; R = 675 nm; FR = 675 + 725 nm

red light. Red and far-red stimulated increase of radioactivity of 36 kd form in *P. aquilinum* was cancelled by cycloheximide (Fig. 2a).

Electron microscopic investigation

Plastids of protonemal cells of *P. aquilinum* (Figs 3a, b, c) are abound in both grana and stroma thylakoid. The red light was not effective to induce differences in the structure of inner membrane system. There were many lipid drops in apical cells.

The cells of *D. filix-mas* contained proplastids in darkness and also after illumination with far-red light (675 + 725 nm). Prolamellar bodies and inner lamellae were not found (Figs 3d, f). The red light illumination (675 nm) resulted some little grana with 2–4 thylakoids (Fig. 3e). The vacuolation apparently increased in these cells. The cytoplasm was full with lipid bodies in both dark and light treated samples.

A characteristic phytochrome effect was the more intense osmiophilic character of mitochondrial and chloroplast stroma as compared with the cytoplasm. This difference was observed in both species after red light treatment.

Table 2

Statistical analysis results obtained in labelling of 29 kd[a] and 36 kd[b] polypeptides during the light and drug treatment in fern gametophytes

Treatments	*t* statistics		Significance of *t*	
	29 kd of *P. aquilinum*	36 kd of *D. filix-mas*	29 kd of *P. aquilinum*	36 kd of *D. filix-mas*
D				
C–CH	0.96	2.30	>0.30 N.S.	<0.05 S.
C–CAP	0.70	2.06	=0.50 N.S.	<0.10 S.
C–Act-D	0.82	2.02	>0.40 N.S.	<0.10 S.
CH				
D–R	0.30	2.35	>0.70 N.S.	<0.05 S.
D–FR	0.37	0.31	>0.70 N.S.	>0.70 N.S.
R–FR	0.03	2.13	>0.90 N.S.	<0.10 S.
CAP				
D–R	2.08	1.15	<0.10 S.	>0.20 N.S.
D–FR	0.02	0.04	>0.90 N.S.	>0.90 N.S.
R–FR	2.05	1.72	<0.10 S.	>0.10 N.S.
Act-D				
D–R	3.55	4.06	<0.01 S.	<0.01 S.
D–FR	0.35	0.76	>0.70 N.S.	>0.40 N.S.
R–FR	5.63	3.53	<0.001 S.	<0.01 S.

Abbreviations as in Table 1
[a] 29 ± 1.5 kd
[b] 36 ± 1.8 kd

Discussion

Differentiation of the young fern gametophyte begins before spore rupture. Three cells, which differ in structure and function are developed during the germinating processes. The first visible steps leading to rhizoid inception are preceded by a sequence of biochemical changes in the spore. The early stage of spore germination can be divided into three phases. During the pre-induction phase the spore imbibes water and a sensitivity to light is established, oxidative processes are involved and proteins required for the next phase are synthesized at this time. During the induction phase the spores are sensitive to light exposure which induces a series of photochemical reactions. These in turn bring about morphogenetic processes leading to the formation of rhizoidal and protonemal cells during the post-induction phase

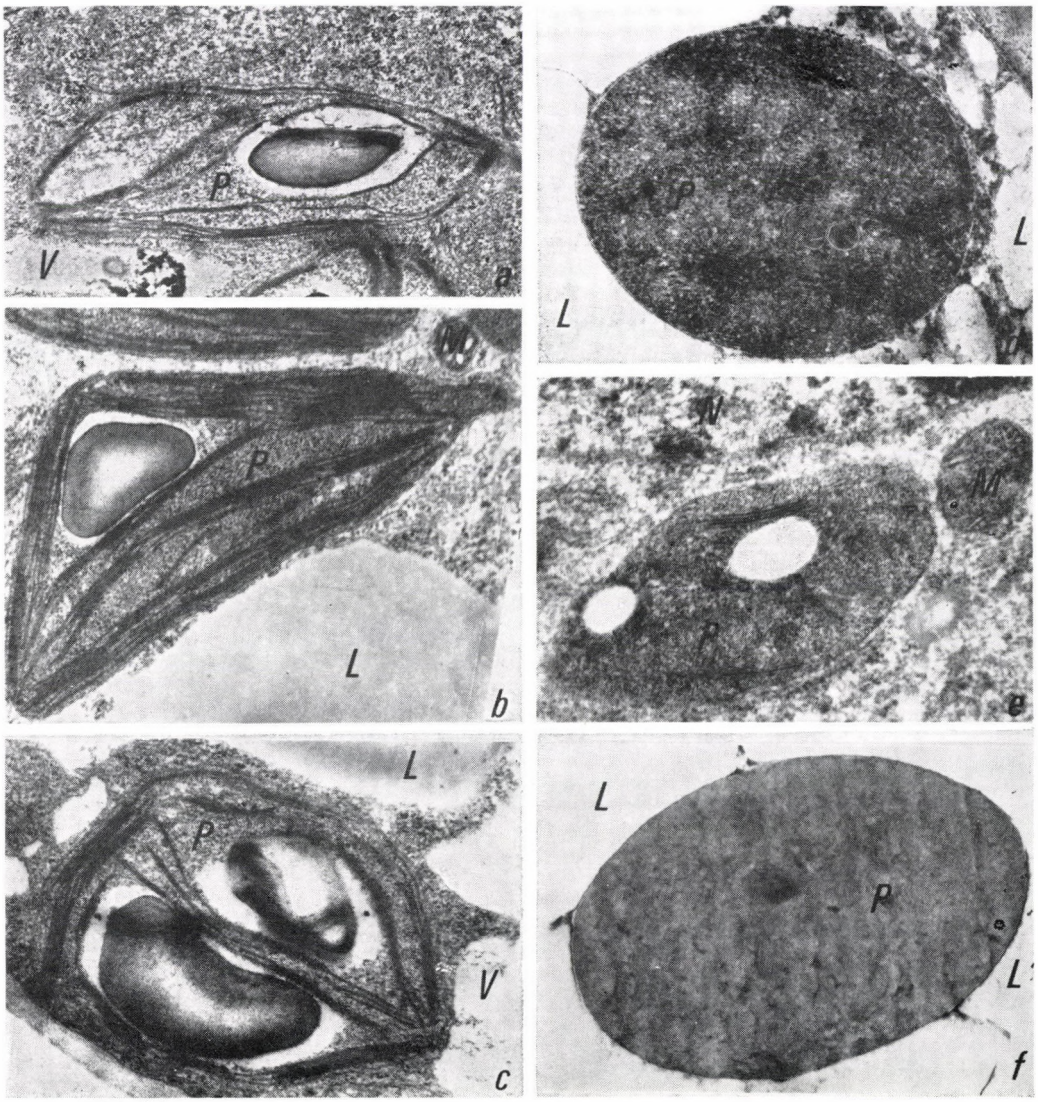

Fig. 3. Electron microscopic pictures of plastids of 144 h old gametophytes in darkness (a, d) and after illumination with red (b, e); far-red (c, f) light. *Pteridium aquilinum* (a, b, c); *Dryopteris filix-mas* (d, e, f). Magn. a: ×14 400; b: ×29 000; c: ×30 000; d: ×28 500; e: ×31 100; f: ×30 600. P = plastid; M = mitochondrion; L = lipid drop; V = vacuole; N = nucleus

(Towill and Ikuma 1975a, b, c). Raghavan (1970, 1971a), De Maggio and Raghavan (1972) investigated the regulation of protein and RNA synthesis during rhizoid initiation and elongation of the cell in *P. aquilinum*. They concluded that rhizoid and protonemal cell initiation requires the synthesis of proteins coded on preformed messenger RNA already present in the spore,

whereas elongation of these cells requires additional proteins coded on newly synthesized messenger RNA.

The induction phase has received more attention than any other aspect of spore germination. With a few exceptions fern spores require irradiation with visible light in order to germinate. *P. aquilinum* is one of the few exceptions (MILLER 1968). Nevertheless, this species is also sensitive to irradiation, since successful synchronization has been achieved by light treatments (RAGHAVAN 1970).

The light stimulated growth and development are special aspects of photomorphogenesis. Several workers reported action spectra of various photomorphogenetic phenomena in fern gametophytes. The first detailed analysis of a photomorphogenetic response was provided by MOHR (1956) on prothallial growth in *D. filix-mas*. Recently SUGAI (1971) and WADA and FURUYA (1974) estimated an action spectrum for spore germination in *Pteris vittata* and in *Adiantum capillus-venesis*. They found that a number of developmental cytological and biochemical events in fern gametophytes were subject to photoregulation by blue light. Other photomorphogenetic processes appear to be under phytochrome mediated control, showing the classic red/far-red reversibility. These include spore germination, protonema elongation, timing of cell division and antheridium formation (RAGHAVAN 1971b, 1973, MOHR 1956, MOHR et al. 1964, SUGAI and FURUYA 1967, SUGAI et al. 1977).

Our previous studies on red/far-red reversibility in protein synthesis of germinating *P. aquilinum* and *D. filix-mas* spores was found to be phytochrome regulated in the case of 42 kd as well as of 36 kd and 29 kd polypeptides respectively (NAGY et al. 1978).

Development of photosynthetic structures and functions are an early event during the germinating process (MOHR et al. 1964). According to APEL (1979) some of the thylakoid polypeptides of chloroplast are also under phytochrome mediated control. Consequently the light induced protein synthesis in our experiments are probably connected this way with the photosynthetic functions. This assumption seems to be supported by the electron miscroscopic pictures of chloroplast of red light treated *D. filix-mas* (Fig. 3).

In general membrane system of protonemal chloroplasts of ferns is similar to that of the angiosperms to some extent in a simplified form. In *Dryopteris pseudo-mas* it has been demonstrated that the average number of plastid per cell remains remarkably constant for the first four or five protonemal cells (CRAN 1970). In the fern gametophyte therefore, plastid replication can be followed through more cell generations than in an angiosperm (CRAN 1979). Thus, it cannot be excluded that most of the light induced protein synthesis is connected with the chloroplasts, especially with the synthesis and assembly of the thylakoid membrane system. These processes are controlled both by nuclear and by organellar genes. Light regulated gene

expression can be achieved at the level of transcription or translation (PARTHIER 1982).

In our experiments red light controlled organellar synthesis was found in the case of 36 kd polypeptide in germinating spores of *D. filix-mas*. The effect of chloramphenicol indicate an organellar translation. A polypeptide with similar molecular weight (37 kd) is known to be a component of the cytochrom b_6 complex of thylakoid-membrane. It is coded by the chloroplast DNA, and synthesized inside the chloroplasts (DOHERTY and GRAY 1979). Nuclear coding site and synthesis on cytosolic polysomes are known for the 29 kd component of light-harvesting chlorophyll protein complex (HERRMANN et al. 1980, WETTSTEIN 1981). We observed a phytochrome induced synthesis of a similar polypeptide in *P. aquilinum* gametophyte. This induction appears to be inhibited by the treatment with cycloheximide (Table 2 and Fig. 2a).

The 42 kd polypeptide was found to be regulated by active phytochrome in both investigated species. The effect of red light was inhibited by cycloheximide. Among thylakoid polypeptides a 44 kd unit is known in photosystem I. It is coded in the nucleus and synthesized in the cytosol (NECHUSHTAI et al. 1981, CHUA and GILLHAM 1977). In our experiments the incubation of spores with actinomycin-D prevented the red light stimulation of the 42 kd polypeptide in the case of *D. filix-mas* gametophyte only. These results indicate that the light dependency of germination may be connected with a change in level of phytochrome regulation (transcriptional vs. translational) during the evolution.

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AN ALTERED CONCEPT OF THE MODEL OF THE BINDING SITES FOR TRIAZINE IN *AMARANTHUS RETROFLEXUS* L. AND *SENECIO VULGARIS* L.

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Introduction

In recent years, there have been several reports of the occurrence of weeds resistant to the triazines (RYAN 1970, BANDEEN and MCLAREN 1976, THOMPSON, SCHUMACHER and RIECK 1974). The common aspect of all these plants is that they were found in areas of agricultural production where triazines were used repeatedly with little or no rotation with other, non-triazine herbicides (PFISTER and ARNTZEN 1979). Competitive binding studies conducted with radiolabeled herbicides have suggested that s-triazines, triazinones, pyridazinones, biscarbamates, phenylureas, N-phenylcarbamates, uracils, acylanilides, cyclic ureas and thiadiazoles interfere with the same electron carrier of the electron transport chain through a similar mechanism (MORELAND 1980). It has also been suggested that these herbicides interrupt photosynthetic electron transport by acting at the level of B, the second electron carrier on the reducing site of photosystem II (PFISTER and ARNTZEN 1979). ARNTZEN, DITTO and BREWER (1979), PFISTER, RADOSEVICH and ARNTZEN (1979) as well as RADOSEVICH, STEINBACK and ARNTZEN (1979) have characterized the site of action of photosystem II herbicides, and based upon these results, a model for the binding of inhibitors to the photosystem II-complex was suggested (PFISTER and ARNTZEN 1979, PFISTER, RADOSEVICH and ARNTZEN 1979). However, our parameters calculated for the triazine binding in triazine-resistant and susceptible redroot pigweed (*Amaranthus retroflexus* L.) plants did not match data obtained by PFISTER, RADOSEVICH and ARNTZEN (1979) as well as RADOSEVICH, STEINBACK and ARNTZEN (1979) from analysis of electron transport ($H_2O \rightarrow$ DCPIP) in common groundsel (*Senecio vulgaris* L.) chloroplasts in the presence of various concentrations of triazine. Hence, based upon the model suggested by PFISTER and ARNTZEN (1979), and the differences of the inhibitor binding in the two species, an altered concept of the model of the binding sites for triazine in *Amaranthus retroflexus* L. and *Senecio vulgaris* L. is presented.

Materials and methods

Seeds of the triazine-susceptible *Amaranthus retroflexus* L. biotype were collected from an area where no herbicides of the triazine group had ever been applied. Resistant material was obtained from maize fields where triazines had been used repeatedly with no rotation with other herbicides. Plants were grown in soil for 6 to 8 weeks in a greenhouse. Six plants from each biotype were selected at random and studied separately.

Chloroplasts were isolated in the medium as described by REEVES and HALL (1973). Photochemical activity of photosystem II was determined by measuring the kinetics of light-dependent reduction of 2,6-dichlorophenol indophenol (VERNON and SHAW 1959) in an Aminco DW-2 spectrophotometer in the presence of various concentrations of triazine [2-chloro-4-(ethylamine)-6-(isopropylamine)-S-triazine] or DCMU [3-(3,4-dichlorophenyl)-1,1-dimethylurea]. The herbicides were added to the samples as methanol solutions so that the final

methanol concentration did not exceed 3%. Chlorophyll concentration in the samples was low (6 μg/ml) in order to measure the herbicide inhibition constants accurately (TISCHER and STROTMANN 1977).

Binding constants and interaction between the herbicide binding sites were characterized by the Hill-equation on the basis of the equation given by PFISTER, RADOSEVICH and ARNTZEN (1979):

$$\log \vartheta - \log (1 - \vartheta) = \log K + n \log [L]$$

where ϑ is the fraction of binding sites occupied, K is the binding constant, $[L]$ is the herbicide concentration, and n is the HILL coefficient reporting on the substructure of the binding site.

Results and discussion

Table 1 presents parameters of herbicide binding sites for DCMU and atrazine in *Amaranthus retroflexus* L. and *Senecio vulgaris* L. plants.

The results obtained on effects of DCMU on electron flow in isolated redroot pigweed chloroplasts were found to be the same as those with common groundsel. As pointed out by PFISTER, RADOSEVICH and ARNTZEN (1979), HILL coefficient values of unity indicate independent binding of a single herbicide molecule. The same holds true in respect of the triazine binding site in common groundsel. Based upon the HILL coefficients of unity difference cannot be postulated between the characteristics of binding sites for triazine and DCMU in common groundsel chloroplasts. On the other hand, the binding site for triazine in redroot pigweed certainly differs from that in common groundsel. HILL coefficient values smaller than 1 (0.82 in susceptible, 0.66 in resistant plants) namely suggest that more than one inhibitor molecules take part in the binding process. This is also supported by the data on *Amaranthus*

Table 1

Binding constants (K) and Hill coefficients (n) calculated from Hill plots of data obtained from analysis of electron transport ($H_2O \rightarrow$ 2,6-dichlorophenol indophenol) inhibited by various concentrations of herbicides in chloroplasts of triazine-susceptible and resistant plants (correlation coefficients in regression analysis were between 0.96 and 1.00). Hill activity expressed in mole dye reduced/mole chlorophyll × hour

Plant	DCMU		Triazine	
	K	n	K	n
Amaranthus retroflexus L.				
susceptible	7.22	1.00	5.32	0.82
resistant	7.06	1.06	2.59	0.66
Senecio vulgaris L.				
susceptible	—	1.14*	6.70*	1.07*
resistant	—	1.09*	4.28**	1.04**

Data on *Senecio vulgaris* L. were calculated from the figures of PFISTER, RADOSEVICH and ARNTZEN (1979)* and RADOSEVICH, STEINBACK and ARNTZEN (1979)**, respectively.

(0.82 in susceptible, 0.90 in resistant plants) calculated from the figure of ARNTZEN, DITTO and BREWER (1979).

It is also shown in Table 1 that the binding constants in the resistant redroot pigweed chloroplasts are smaller than those in the common groundsel ones. Inhibitor molecules more than one certainly take part in reducing binding forces in the redroot pigweed chloroplasts.

On the basis of these results an altered concept of the model of the binding sites for triazine, regarding the differences in *Amaranthus retroflexus* L. and *Senecio vulgaris* L., is set up (Fig. 1). The model includes the conception of PFISTER and ARNTZEN (1979) in which the existence of two domains determining binding properties is emphasized; one domain is responsible for binding of the "*essential element*" of the herbicide, the other for binding of the "*specificity determining substituents*". Successful inhibition of electron transport requires interaction of the herbicides with both binding site domains.

In our model the binding sites for DCMU neither in the two species nor in the resistant and susceptible plants differ from one another. The binding of triazine in susceptible common groundsel plants is very similar to that of DCMU: the HILL coefficient value of unity indicates independent binding of a single herbicide molecule. In turn, the two domains in the susceptible redroot pigweed plants may fall nearer or farther than in common groundsel plants, and this makes impossible the interaction of a single herbicide molecule with both binding site domains. Based upon the HILL coefficient smaller than 1 we suggest that in this case two triazine molecules take part in the inhibitory

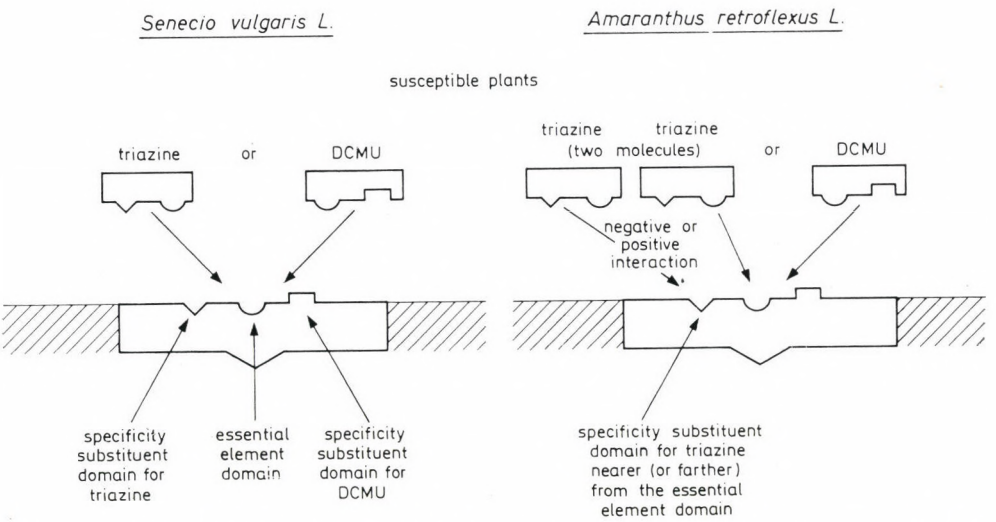

Fig. 1. An altered concept of the model of the binding sites for triazine in *Senecio vulgaris* L. and *Amaranthus retroflexus* L.

effect. Most likely the opposite poles (or different residues) of the molecules may interact with the two domains. The binding forces between the two domains and the herbicide molecules (which may repel or attract one another) are evidently smaller than in the case of *Senecio* plants. This is also supported by the smaller binding constants measured in *Amaranthus* chloroplasts.

In resistant plants the alteration of the "*specificity domain*" causes limited triazine binding to it, and this does not allow successful inhibition. However, the presence of weak binding for triazine to the "*essential element domain*" in the resistant chloroplasts is imaginable. In consequence of the weak binding forces the HILL coefficient values of the resistant plants have not such a probative value as those of the susceptible ones.

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3-METOXYCARBONYLMETHYLBENZOTHIAZOLIUM BROMIDE AS INDUCING AGENT FOR PLANT CELL DEDIFFERENTIATION IN VITRO

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3-Metoxycarbonylmethylbenzothiazolium bromide (MMB) induced the callogenesis on the decapited apical segments of the primary root of *Vicia sativa* L. var. *Solarka*. Significant transformation of the plant tissue and of the cells occurs in the elongating zone of the root at the concentration of 10^{-3} mol · dm^{-3}. The fresh mass of the induced calluses is evidently increased.

Introduction

It is well known that growth regulating agents (hormonal effectors) influence not only growth, but also the differentiation and dedifferentiation of plant cells in vitro as well as in vivo.

For inducing dedifferentiation, in most cases synthetical auxinoids are used, as beta-indolylacetic acid (IAA), alpha-naphtylacetic acid (NAA), indolylbutyric acid (IBA), 2,4-dichlorphenoxyacetic acid (2,4-D), kinin derivatives, gibberellin retardans and other substances, which induce meristematization of the differentiated cell, influence cell division and the single phases of the mitotic cycle, being inevitable for maintaining non-organized growth of a tissue culture.

In the last years it has been proved that also other synthetic auxinoids of the indolyl row have regulating effects, besides the above-mentioned substances. Substituting carbonium by a nitrogen atom in the indole ring (indene-3-acetic acid), the ability of the compound is preserved for influencing the elongating growth of coleoptole segments (THIMANN 1969). In a similar way active compounds as auxin arise by substituting the pirole ring of indole by a thiazole ring and its binding to the phenyl ring (GIANNELLA et al. 1971). Some of them, e.g. benazoline (4-chloro-2-oxo-benzothiazoline-3-acetic acid) are at the initiation and the growth of calluses just as active as 2,4-D or even surpass it (INGRAM et al. 1972). Benzothiazolilacetic acid stimulates the growth of a tissue culture of the mint, analogically as alpha-naphthylacetic acid (LAMBA et al. 1963).

It has been found out that also 2-R-3-R′-substituted benzothiazolium salts show regulating activity (SUTORIS et al. 1980). Among them, e.g. MMB* is an efficient growth stimulator similarly to IAA (SEKERKA 1983), therefore it became the theme of further studies.

Material and methods

Callogenesis was induced at apical segments of the primary roots of *Vicia sativa* L. var. *Solarka*.

Selected seeds (of approximately equal size and colour of the seed envelope) were sterilized in 70% ethanol for 15 minutes. To increase sterility, the seeds were moreover treated

* MMB = 3-metoxycarbonylmethylbenzothiazolium bromide.

by a high frequency corona discharge for 20 minutes. The sterilized seed germinated in Petri dishes on 0.8% agar nutrient medium for 48 hours in the dark, at a temperature of 25 ± 1 °C.

For the further experiment, sterile seedlings of the length of 25–30 ± 1 mm were used. Therefrom the apical segments of primary roots were decapitated at a length of 10–15 mm, which were planted into Petri dishes in horizontal position on a 0.6% modified solid agar nutrient medium according to MURASHIGE-SKOOG (1962). In the experimental variants, the medium contained MMB in concentrations of 10^{-13}–10^{-2} mol · dm^{-3}. In the control variant, the nutrient medium did not contain any hormonal substances.

After the fresh mass of the apical segments of the primary roots had been determined, callogenesis was induced at a temperature of 25 °C in the dark for 14 days. Preparing of the model material as well as cultivation were made under aseptic conditions. Increasing of the fresh mass during callogenesis was stated gravimetrically. Morphogenic changes are documented photographically.

Results and discussion

As it is shown in Plate I, callogenesis is induced of the plant tissue during the cultivation of the decapitated segments on the solid agar medium.

Under control conditions, without hormonal effectors (Plate I/a), the length of the apical root segments increases as a consequence of elongating and embryonal growth. By treating with the studied substance at concentrations of 10^{-11}–10^{-7} mol · dm^{-3}, prolongating growth of the roots is stimulated. It is expressed also by increasing of the fresh mass (by 8.79% at the concentration of 10^{-7} and by 7.68% at the concentration of 10^{-7} mol · dm^{-3} respectively) when compared with the control (Fig. 1).

More concentrated solutions of the investigated substance inhibit the elongating growth. Significant transformation of the plant tissue and of the cells occurs at the concentration of 10^{-3} mol · dm^{-3}.

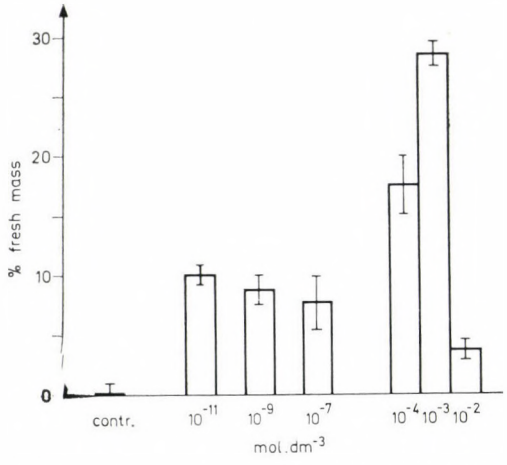

Fig. 1. Percentage of the fresh mass of the roots of *Vicia sativa* on the 14th day of callogenesis induced by MMB

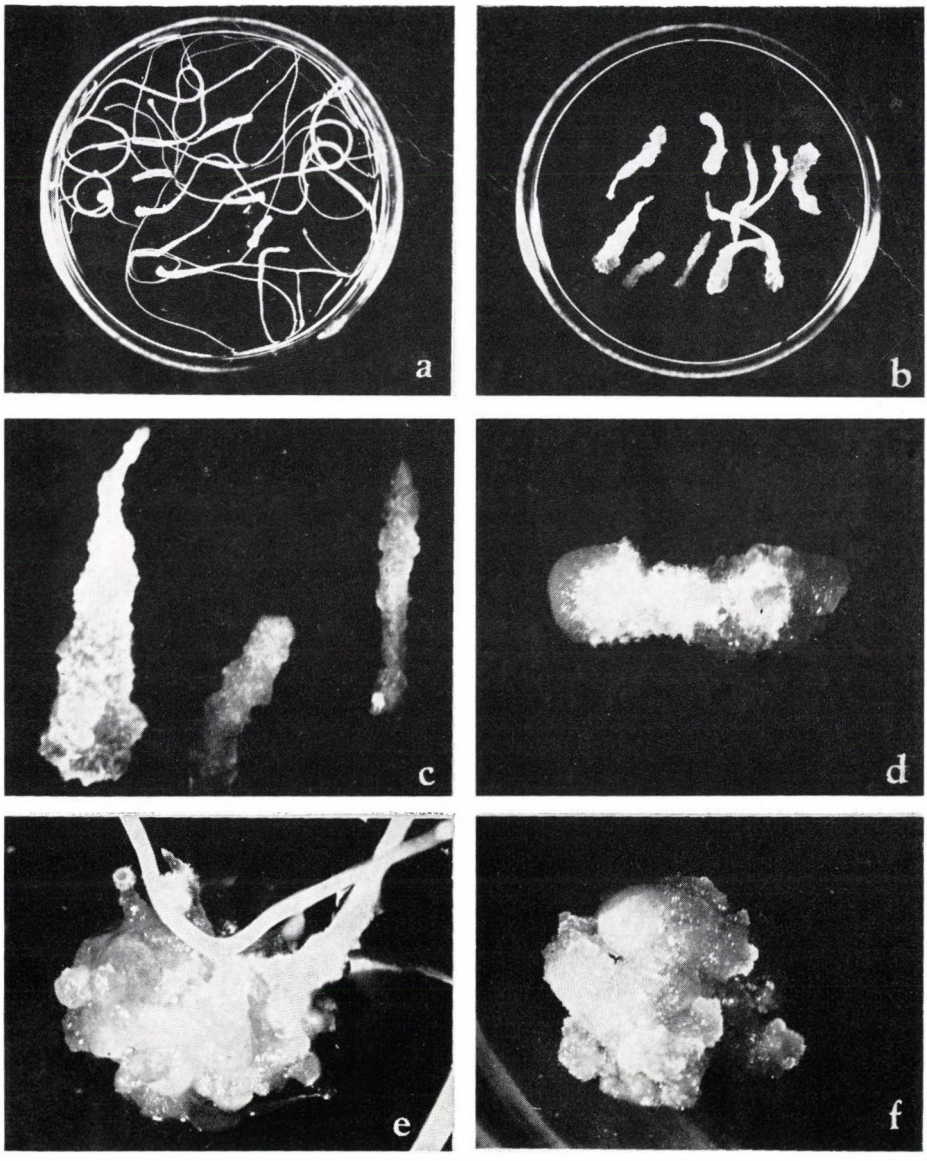

Plate I

Callus induction on decapitated segments and intact seedlings of *Vicia sativa* under the influence of MMB

In the series of experiments with decapitated root segments (Plate I/b, c), dedifferentiation of the tissue occurred in most cases in the elongating zone of the root. Later, after transferring on a fresh medium of analogical composition, step by step also the meristematic zone dedifferentiated (Plate I/d).

Elongating growth is evidently lowered. By dedifferentiating processes callus is formed. The fresh mass of the induced calluses increased by $28.83 \pm 1.14\%$ (Fig. 1).

In the experimental series with intact vetch seeds, sown on agar medium, an analogical effect occurs after the treatment with the studied substance at the single concentrations, as with the decapitated root segments. After influencing with the substance in the concentration of 10^{-3} mol · dm^{-3}, the callus is initiated at the boundary between the epicotyl and the hypocotyl of the seedling (Plate I/e). The calluses formed in this way are of cream coloured yellow shape. At the state of the primocallus, the bonds between the single cells are relatively weak, the callus is friable.

After transferring the primocallus on to a fresh medium of analogous composition, the callus maintains its typical non-organized growth (Plate I/f), which can be used for further experiments.

Our results point at the possibility of using 2-R-3-R′-substituted benzothiazol salts also in transformation of plant cells and tissues.

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CONCENTRATIONS OF PHOTOSYNTHETIC PIGMENTS IN A TURKEY-OAK FOREST AND AT ITS EDGE

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Concentrations of chlorophyll a and b and carotenoids have been studied in the leaves of the dominant tree and shrub species of a turkey-oak forest and its edge. Inside the forest, depending on the vertical distribution of light, the concentration of all pigments in the dry matter is much higher in the leaves of the shrub species then in those of the tree species. At the forest edge, the increase of concentrations towards the lower levels is less pronounced because the two levels differ to a lesser extent in the light quantity available. Due to the higher light intensity, at the edge the concentration of pigments in the dry matter considerably decreases if compared to the forest interior. Due to the differences in leaf anatomy, however, the pigment concentrations per unit leaf surface are often higher in this habitat. The chlorophyll a : b ratio indicates the differences in the spectral composition of light. This ratio is generally lower in the forest interior than at the forest edge. Also, it is lower in the leaves of shrubs than in those of the trees in both habitats.

Introduction

In affecting the composition, physiognomy and functional characteristics of the marginal vegetation developed at the border of a forest stand and a non-forested area, the light conditions differring considerably from those inside the forest are of decisive importance (WALES 1967, RANNEY 1977). In addition to the shade-intolerant species, shade-tolerants common within the stand also occur. The adaptation to the two habitats differing in light conditions and other environmental factors implies biochemical and anatomical changes of the physiological and photosynthetic apparatus of shade-tolerant species. These changes in adaptation cause the ecological variability of photosynthesis (GORYSHINA 1980). Since out of the physiological processes photosynthesis (which provides chemical energy and substrata for all subsequent biosyntheses in the plant) is the most sensitive to the change of environmental conditions (mainly that of the light), the photosynthetic apparatus strives to adjust itself to the particular environment in such a manner that the available light energy be utilized most effectively (BJÖRKMAN and HOLMGREN 1963). BJÖRKMAN (1968a, b) and BOARDMAN (1977) emphasize that the extent of physiological, biochemical and anatomical changes is determined by genotypes and depends on the evolution of the given species and ecotype. The explanation of the different photosynthetic responses of the same species found in habitats with different light conditions needs the quantitative and qualitative analysis of photosynthetic pigments. The present paper deals with the chlorophyll and carotenoid concentrations in the leaves of the dominant tree and shrub species present both in the interior of a turkey-oak forest (low light intensity) and at its edge (high light intensity).

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The study area

The investigations have been carried out in a turkey-oak forest (*Quercetum petraeae-cerris*) and at its NW edge vegetation formed at the border of an agricultural land (Síkfőkút Project, Hungarian Research Area of MAB). The structure of the forest and its marginal vegetation is described in detail by JAKUCS, HOVÁTH and KÁRÁSZ (1975), PAPP and JAKUCS (1976) and MÉSZÁROS, JAKUCS and PRÉCSÉNYI (1981), among others.

Material and method

The concentrations of photosynthetic pigments were measured in the leaves of the dominant tree species (*Quercus petraea*, *Quercus cerris*) and shrub species (*Ligustrum vulgare*, *Acer tataricum*, *Cornus sanguinea*, *Euonymus verrucosus*) of the forest and its marginal vegetation. In both places 10 leaves from each of 5 individuals per species were collected at each point of time, and the 50 leaves obtained were treated as a mixed sample. In case of trees the samples were taken from the lower canopy level (shade level).

The pigment concentrations were determined in 3×7 leaves of each species in the following way: from the middle part of both halves of each leaf-blade 2 disks were taken by a drill of 0.7 cm in diameter, one disk was used for pigment studies while the other for determining dry matter content. The extraction and determination of pigments were carried out following CZUCHAJOWSKA and PRZYBYLSKI (1978). The extraction was done in a braying mortar using quartz sand and $MgCO_3$, and 100% acetone. The light absorption of the extracts was measured at wavelengths of 662, 644 and 440.5 nm. Care was also taken in measuring the turbidity as it can result in erroneously high pigment concentrations (WATTS and ELEY 1981). To correct the values measured at the previous wavelengths with the absorption values measured at a wavelength of 750 nm (where the chlorophylls do not absorb light any more), the concentration of chlorophyll a and b as well as that of the carotenoids were calculated by HOLM's formulae (HOLM 1954) used also by WATTS and ELEY.

Results and discussion

Chlorophylls

After the summer maximum (June 17 or July 7) the concentrations of chlorophyll a and b given for unit dry-matter weight (Table 1) and for unit leaf surface (Table 2) decrease in the interior of the forest as well as at the forest edge.

Similarly to the results of previous investigations carried out in the forest (TUBA 1977, TUBA and NYILAS 1980), a characteristic vertical distribution of the concentration of chlorophyll a and b related to dry matter was observed. In the leaves of the species of the tree stratum, especially in *Quercus petraea*, the concentration of both pigments is lower than in the leaves of shrubs. The intensity of the light filtered through the tree stratum decreases so that photoreceptors receive less light. Consequently, larger amounts of chlorophylls are synthetized to utilize effectively the weaker light. At the forest edge, a small increase of concentrations towards the lower levels is also observed. Here, the light quantity available for photosynthesis by the species constituting the two levels does not differ to such a large extent than in the interior of the forest.

The stronger light intensity at the edge evokes a strong decrease of the concentration of chlorophyll a and b related to dry matter in the leaves of shrubs. A similar change was indicated in the species of the tree stratum, to a lesser extent in *Quercus petraea* and to an

Table 1

Concentrations of chlorophyll a and b related to dry matter
(in mg/g)

Species		Time					
		17. 06.	07. 07.	04. 08.	17. 08.	09. 09.	14. 10.
Forest interior							
Ligustrum vulgare	chl a	5.9932	7.1228	6.6116	5.6381	6.1158	5.0828
	chl b	2.6914	3.3673	3.0214	3.8034	2.8680	1.8033
Acer tataricum	chl a	6.5826	8.0550	5.5328	6.1642	5.6784	3.9950
	chl b	3.2183	3.6471	2.2471	3.0194	2.4845	1.6804
Cornus sanguinea	chl a	6.9086	8.5272	5.9457	6.4017	5.6543	3.8952
	chl b	3.1662	4.1834	2.3556	2.6212	2.2889	1.3191
Euonymus verrucosus	chl a	7.5926	8.4098	6.8221	7.2028	5.8391	5.9937
	chl b	3.4353	3.8050	3.2978	3.5019	2.3447	2.6785
Quercus petraea	chl a	3.5955	4.4821	—	3.9582	3.7426	3.0744
	chl b	1.5509	1.9306	—	1.6604	1.1595	1.2209
Quercus cerris	chl a	6.6100	7.8481	—	5.5992	4.9267	4.4167
	chl b	2.9496	3.3517	—	2.5326	1.4292	1.5176
Edge of the forest							
Ligustrum vulgare	chl a	3.6180	3.9646	3.1651	3.3060	2.1677	1.8991
	chl b	1.7681	1.2767	1.2440	1.4687	0.6973	0.4852
Acer tataricum	chl a	4.4691	4.8917	4.1802	4.8849	3.5906	1.7578
	chl b	2.1546	2.4580	1.6548	2.1079	1.6150	0.6200
Cornus sanguinea	chl a	4.5511	4.5692	3.8290	4.1050	2.4367	1.6908
	chl b	2.1862	2.1693	1.1011	1.2839	0.9430	0.2876
Euonymus verrucosus	chl a	5.1222	5.9671	4.7642	5.7086	4.5505	3.5237
	chl b	2.3493	2.7609	1.7451	2.2809	1.5108	1.0987
Quercus petraea	chl a	2.7395	3.5977	—	3.4455	3.4672	2.8367
	chl b	0.8787	1.4121	—	1.1298	1.0430	0.9469
Quercus cerris	chl a	4.0603	4.1279	—	3.0945	3.0336	2.2845
	chl b	1.7759	1.6434	—	0.9528	0.8948	0.8198

extent close to that in the shrubs in *Quercus cerris*. At strong light intensity the synthesis of chlorophyll a and b in a larger concentration would not only be unnecessary but deleterious as assumed by JONES and KOK (1960), since the sensitivity of the photochemical reaction centres to photoinhibition increases with the increasing proportion of the pigments related to the reaction centres.

If calculated for unit leaf surface, the chlorophyll a and b concentrations decrease to a larger extent in the interior of the forest and to a smaller extent at the edge. All this can be explained with leaf anatomical changes as pointed out by several authors dealing with leaves and plants exposed to different intensity of light (HOLMGREN 1963, BAUER and BAUER 1980, GORYSHINA 1980, LARCHER 1980, HOFLACHER and BAUER 1982). At the margin, where the intensity of light is high, the amount of dry matter per a leaf surface of 100 cm^2 is higher in all cases as compared to the forest interior of low light intensity (Table 3). The leaf-blades are thicker due to the increase in the number of cell layers of the palisade and loose clorenchyma.

If compared to the interior, at the edge the increase of dry matter is larger than the decrease of chlorophyll a and b concentration related to unit dry matter weight. Therefore,

Table 2

Concentrations of chlorophyll a and b related to unit leaf surface (in mg/100 cm²)

Species		Time					
		17. 06.	07. 07.	04. 08.	17. 08.	09. 09.	14. 10.
Forest interior							
Ligustrum vulgare	chl a	2.6041	2.3607	2.1458	2.2729	1.8663	1.9686
	chl b	1.1715	1.1084	0.9683	1.5492	0.8667	0.7028
Acer tataricum	chl a	2.1615	2.1153	1.8012	1.9800	1.8145	1.6463
	chl b	1.0114	0.9608	0.7370	0.9694	0.7920	0.6941
Cornus sanguinea	chl a	2.0563	2.2369	2.1498	2.0448	1.7229	1.0617
	chl b	0.9283	1.0973	0.8557	0.8479	0.7030	0.3925
Euonymus verrucosus	chl a	1.8268	1.9020	1.8215	1.8418	1.6685	1.3139
	chl b	0.8233	0.8627	0.8764	0.8862	0.6639	0.5866
Quercus petraea	chl a	1.6775	2.2153	—	1.9446	1.7538	1.4852
	chl b	0.7233	0.9522	—	0.8373	0.5458	0.5921
Quercus cerris	chl a	2.0084	2.1875	—	2.1751	2.1761	1.6981
	chl b	0.8925	0.9382	—	0.9738	0.6657	0.5835
Edge of the forest							
Ligustrum vulgare	chl a	1.9940	2.4631	2.2330	2.2910	1.3941	1.1794
	chl b	0.9227	0.8162	0.8751	0.9961	0.4513	0.2943
Acer tataricum	chl a	2.2518	2.4900	2.2614	2.1912	1.7667	0.8918
	chl b	1.0767	1.2568	0.9004	0.9467	0.7793	0.3048
Cornus sanguinea	chl a	2.0538	1.9013	1.9588	2.1272	1.4425	0.6112
	chl b	0.9862	0.9072	0.8499	0.6663	0.5578	0.1259
Euonymus verrucosus	chl a	2.2320	2.2561	1.9123	2.2986	1.6822	1.1686
	chl b	1.0245	1.0416	0.7036	0.9281	0.5605	0.3675
Quercus petraea	chl a	1.8225	2.4660	—	2.3970	2.2485	1.7404
	chl b	0.5326	0.9573	—	0.7841	0.6669	0.5814
Quercus cerris	chl a	2.7627	3.1566	—	2.5734	3.0007	2.1402
	chl b	1.1997	1.2586	—	0.8103	0.9181	0.7702

the concentration values given for unit leaf surface are frequently higher. This is supported by BOARDMAN's (1977) statements that plants use a larger fraction of their synthetizing capacity in making and maintaining the light-collecting apparatus in habitats of lower light intensity than in those of higher light intensity. This also means that the fraction of the available chemical energy used for the synthesis of components determining the effectiveness of light absorption is larger in the shade-tolerant plants grown at low light intensity, as compared to the fraction used for the synthesis of components determining the capacity of enzymatic steps. Thus, the activity of carboxydismutase which is important in CO_2 fixation, and the activity of other photosynthetic enzymes are low in these plants (BJÖRKMAN 1968a).

The increase in leaf thickness at high light intensities and its consequence, the increase of the leaf volume per unit leaf surface were brought into connection with the increased CO_2 fixation capacity (BOARDMAN 1977).

The spectral composition of the photosynthetically active radiation (PHAR) influences the proportion of chlorophyll a and b. The chlorophyll a : b ratio is usually lower in the interior of the forest than at its edge and, at the same time, lower in the leaves of shrubs than in the trees in both places (Table 4).

Table 3

Quantities of dry matter related to unit leaf surface
(in g/100 cm²)

Species	Time					
	17. 06.	07. 07.	04. 08.	17. 08.	09. 09.	14. 10.
Forest interior						
Ligustrum vulgare	0.3615	0.3194	0.3182	0.4283	0.2956	0.3860
Acer tataricum	0.3107	0.3070	0.3243	0.3474	0.3497	0.3541
Cornus sanguinea	0.2884	0.2711	0.3677	0.3494	0.3469	0.2803
Euonymus verrucosus	0.2377	0.2525	0.2983	0.2477	0.3107	0.2133
Quercus petraea	0.4964	0.5608	—	0.4922	0.4787	0.4874
Quercus cerris	0.4147	0.4345	—	0.4228	0.5279	0.4282
Edge of the forest						
Ligustrum vulgare	0.5343	0.6821	0.7032	0.6174	0.6785	0.6586
Acer tataricum	0.5088	0.5076	0.5311	0.5073	0.4772	0.4750
Cornus sanguinea	0.4506	0.4320	0.5534	0.5274	0.6031	0.4550
Euonymus verrucosus	0.4221	0.3751	0.4395	0.4084	0.3798	0.3113
Quercus petraea	0.6128	0.7205	—	0.7802	0.5666	0.5779
Quercus cerris	0.8567	0.8010	—	0.8988	0.9027	0.8328

Table 4

Chlorophyll a : b ratio in the leaves of the species studied

Species	Time					
	17. 06.	07. 07.	04. 08.	17. 08.	09. 09.	14. 10.
Forest interior						
Ligustrum vulgare	2.23	2.12	2.19	1.48	2.13	2.82
Acer tataricum	2.05	2.21	2.46	2.04	2.29	2.38
Cornus sanguinea	2.18	2.04	2.52	2.44	2.47	2.95
Euonymus verrucosus	2.21	2.21	2.07	2.06	2.49	2.24
Quercus petraea	2.32	2.32	—	2.38	3.23	2.52
Quercus cerris	2.24	2.34	—	2.21	3.45	2.91
Edge of the forest						
Ligustrum vulgare	2.05	3.11	2.54	2.25	3.11	3.91
Acer tataricum	2.07	1.99	2.53	2.32	2.23	2.84
Cornus sanguinea	2.08	2.11	3.48	3.20	2.58	2.58
Euonymus verrucosus	2.18	2.16	2.73	2.50	3.01	2.65
Quercus petraea	3.12	2.55	—	3.05	3.32	3.00
Quercus cerris	2.29	2.51	—	3.25	3.39	2.79

The proportion of the rays of various wavelengths changes in the light filtered through the canopy level (LOOMIS 1965, SMITH 1980) so that the percentage of the rays of shorter wavelengths (green, blue) increases. The higher concentration of chlorophyll b offers an opportunity for utilizing the available weaker light by partially filling up the gap in the absorption spectrum of chlorophyll a absorbing the energy of light with shorter wavelength, and transferring energy to chlorophyll a (DRASKOVITS and FEKETE 1976, IDA 1981).

Carotenoids

Besides chlorophylls, carotenoids represent another important group of photosynthetic pigments. These substances the role of which in photosynthesis and the structure of chloroplasts has not been completely revealed, are called accessory or auxiliary pigments. In addition to their role in absorbing light energy, they provide a protection against the aerobic photo-oxidation caused by intensive light by absorbing rays of shorter wavelength (ANDERSON 1958, IDA 1981). In absence of them singlet oxygen is produced as an intermediate

Table 5

Concentrations of carotenoids related to unit dry matter mass and leaf surface

Species		Time					
		17. 06.	07. 07.	04. 08.	17. 08.	09. 09.	14. 10.
Forest interior							
Ligustrum vulgare	mg/g	2.2277	2.4497	2.2716	1.6716	2.1278	2.0479
	mg/100 cm²	0.9805	0.8080	0.7333	0.6705	0.6347	0.7891
Acer tataricum	mg/g	2.2920	2.8879	2.1350	2.2452	2.2407	1.6492
	mg/100 cm²	0.7198	0.7591	0.6968	0.7163	0.7193	0.6800
Cornus sanguinea	mg/g	2.2181	2.8511	2.2448	1.9226	1.9510	1.5932
	mg/100 cm²	0.6488	0.7471	0.8087	0.6196	0.5962	0.4258
Euonymus verrucosus	mg/g	2.6057	2.8774	2.5933	2.3644	2.1820	2.4897
	mg/100 cm²	0.6278	0.6494	0.6891	0.6041	0.6284	0.5406
Quercus petraea	mg/g	1.2133	1.4971	—	1.2608	1.2887	1.1320
	mg/100 cm²	0.5695	0.7394	—	0.6420	0.6023	0.5514
Quercus cerris	mg/g	2.1885	2.6032	—	1.7387	1.7377	1.6436
	mg/100 cm²	0.6688	0.7244	—	0.6761	0.7654	0.6318
Edge of the forest							
Ligustrum vulgare	mg/g	1.2312	1.0912	1.0816	1.2265	0.8091	0.9030
	mg/100 cm²	0.6786	0.9155	0.7654	0.8642	0.5190	0.5645
Acer tataricum	mg/g	1.6016	1.9026	1.6140	1.3274	1.3788	0.8723
	mg/100 cm²	0.8061	0.9342	0.8714	0.6186	0.6817	0.4382
Cornus sanguinea	mg/g	1.5418	1.8489	1.4122	1.4865	1.0252	0.8157
	mg/100 cm²	0.6958	0.7719	0.7219	0.7710	0.6053	0.3523
Euonymus verrucosus	mg/g	1.8636	2.1274	1.7888	2.1266	1.7340	1.3305
	mg/100 cm²	0.8116	0.8039	0.7168	0.8513	0.6422	0.4391
Quercus petraea	mg/g	0.7666	1.3046	—	1.1839	1.2116	1.0359
	mg/100 cm²	0.5556	0.8916	—	0.8242	0.7863	0.6342
Quercus cerris	mg/g	1.3603	1.3173	—	1.0535	0.9806	0.8206
	mg/100 cm²	0.9219	1.0157	—	0.8746	0.9785	0.7688

energy carrier in the photooxidation of certain forms of chlorophyll. This oxygen is rather reactive and has a damaging influence on membrane components of plastids (AXELSSON et al. 1982). All these emphasize the photoprotective capability of the carotenoids.

The concentrations of carotenoids (Table 5) follow the changes of chlorophyll concentrations during the growth season with a summer maximum. The concentrations remain below the concentration of chlorophyll b, except in the autumn period. In autumn they are higher, particularly at the forest edge. As SANGER (1971) also pointed out, this can be explained by a quicker destruction of chlorophylls and a slower destruction of carotenoids.

Both in the interior and at the edge of the forest carotenoids show a vertical distribution of concentrations similar to that of the chlorophylls.

The concentration of carotenoids related to dry matter is higher within the forest similarly to the chlorophyll concentrations. The difference in the spectral composition of light is also reflected in the concentration of carotenoids, which, together with chlorophyll b, absorb the energy of light with shorter wavelength, ensuring economical utilization of the light spectrum available (LARCHER 1980).

Summary

Due to the different light conditions, the concentration and proportion of photosynthetic pigments differ in the leaves of the dominant tree and shrub species present in both habitats studied. In the interior of the forest the concentration of pigments related to dry matter is much higher in the trees reflecting the vertical distribution of light. At the forest edge, where the between-level difference in the amount of available light is less, the increase of concentrations towards the lower level is less pronounced.

Due to the higher light intensity, the concentration of pigments related to dry matter is much lower at the edge than in the interior of the forest. As a result of differences in leaf anatomy (a thicker leaf-blade, more dry matter), however, the pigment concentrations related to unit leaf surface are frequently higher at the edge.

The chlorophyll a : b ratio indicates the differences in the spectral composition of light. In the interior of the forest it is lower than at the edge and lower in the leaves of shrubs than in the trees in both places.

The present comparative study showed that the occurrence of numerous individuals of the shade-tolerant shrub species in the marginal vegetation is in connection with the anatomical and biochemical adjustment of the photosynthetic apparatus to the light conditions differing considerably from those within the forest. But the question if the photosynthetic capability and the consequent productivity of these species is greater in this habitat has not yet been answered.

When studying the adaptation to habitats, the secondary effects of radiation influencing heat and water balance should also be considered.

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CHANGES OF CAROTENOIDS IN VARIOUS DROUGHT ADAPTED SPECIES DURING SUBSEQUENT DRY AND WET PERIODS*

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Carotenoid transformations of three sandy grassland species (schlerophyllous *Festuca vaginata*, malacophyllous *Achillea ochroleuca* and succulent *Sedum sexangulare*) were investigated during subsequent dry and wet periods (produced by natural drying of the soil and rainlike irrigation). During subsequent short dry and wet periods the drought adapted species show typical carotenoid transformation due to the water shortage. By the examined species from the point of view of their different response to water shortage these symptoms are appearent at a different rate. The carotene content of *Festuca* and *Achillea* increases during dry and decreases during the wet periods. The lutein (+ zeaxanthin) content decreases during dry periods and increases during wet ones. Carotene content of *Sedum* first increases, but from the third (wet) period on it decreases, while its lutein (+ zeaxanthin) content increases continually during all periods. In *Festuca* and *Achillea* among dry conditions the lower amount of violaxanthin is accompanied by a higher amount of antheraxanthin, and vice versa. Violaxanthin content of *Sedum* decreases during dry and increases during wet periods, as well. The neoxanthin quantity of the examined species increases period by period. The changes of the carotenoids (and chlorophylls) among dry and wet ecological conditions may modify also the ratio of pigment systems and the light-harvesting CHL a/b-proteins. By low soil moisture content the schlerophyllous and malacophyllous species, in case of longer drought even the succulent *Sedum* seem to possess higher ratio of pigment system 1 to pigment system 2 and CHL a/b-protein complex.

Introduction

Although many studies have been done on water stress, relatively few are dealing with photosynthetic pigments. From the pigment system components almost exclusively the chlorophylls were studied (VIRGIN 1965, DUYSEN and FREEMAN 1974, 1976, ALBERTE et al. 1975, ALBERTE and THORNBER 1977). Concerning carotenoids, only their total amount was scarcely recorded (DUYSEN and FREEMAN 1974, 1976, SPYROPOULOS and MAVROMMATIS 1978). No detailed information is available on the response of the total photosynthetic pigment system to water deficit. In the knowledge of the high sensibility of the photosynthetic pigments, especially carotenoids, against ecological and internal factors (CLAES 1967, TUBA 1977, ŠESTÁK 1978, GOEDHEER 1979, KRINSKY 1978, IDA 1981), it is obvious that among extreme water deficit the adaptation of photosynthetic pigments should be one of the first steps of plant adaptation.

On this ground it is possible that in the species adapted to water deficit the adaptation of pigment system is controlled by a well established mechanism.

For the investigation of this supposed pigment adaptation three plant species were selected, which are adapted to xeric conditions by different types of water economy. These

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species were studied during subsequent dry and wet periods. Changes of the chlorophylls, carotenes and lutein were reported in our previous study (TUBA 1984). The present paper describes the carotenoid transformations of the three different species in a dry perennial sandy grassland community.

Material and methods

The examinations were carried out in a calciphylous dry perennial sandy grassland community (*Festucetum vaginatae danubiale*) at Vácrátót in the experimental area of the Institute for Botany, in the ssummer of 1981.

Three different drought adapted species of the community were chosen for the investigations: the schlerophyllous *Festuca vaginata* W. et K., the malacophyllous *Achillea ochroleuca* Ehrh. and the succulent *Sedum sexangulare* L. The investigations were carried out in 10×10 m large sampling plots.

The course of investigations

The investigations were carried out after two weeks strong drought period on 28th of July 1981 (dry period), on 29th of July (wet period), on 3rd August (dry period), 4th of August (wet period) and on the 6th of August (dry period). Wet periods during the extraordinary dry summer of 1981 were produced by rainlike irrigation, with an amount of 25–30 mm·m^2 of water supplied during 5 hours before the day of wet periods.

Microclimatic measurements

Air temperature and air humidity (with TZ-18 type of autorecording thermohygrographs) and light intensity (with JU 16 type of photoelectric light meter) were recorded continually at 20 cm height above ground level. Soil temperature (at 5 cm depth) was measured with mercury soil thermometers during the investigation as well.

Water relations determinations

The soil moisture content (0–10 cm) was determined by a direct thermogravimetrical method (SLAVIK 1974), each time with five repetitions.

Leaf water content (expressed in dry weight %) and water saturation deficit (expressed in %) of the examined species were measured according to STOCKER (1929), each time with 10 repetitions by species.

Daily transpiration water loss [expressed in $g \cdot g^{-1}$(dry weight) $\cdot$ day^{-1}] was measured by short time detached leaf weighting method according to IVANOV (1918, 1928) and STOCKER (1929).

Water turnover rate was estimated according to RYCHNOVSKÁ et al. (1972) and expressed in $g \cdot g^{-1}(H_2O) \cdot day^{-1}$. The transpiration rate and the water turnover rate of the examined species were measured in dry and wet period on the same day, from 600 h to 2000 h with intervals of 1 hours.

Photosynthetic pigment determination

Extraction and separation of the pigments were carried out by thin-layer chromatography according MARÓTI and GABNAI (1971), each time with 5 repetitions by the species. The total—pigment extract, obtained by alternating acetonic and petroleum ether procedures, contains the chlorophylls, carotenes and xanthophylls in full. The chloroplast pigments were separated on cellulose powder (MN 300) and silica gel (G to Stahl) thin-layers, with 200–300 μ layer thickness. The chromatograms were developed in dark at 5 °C, applied one-dimensional ascending method in benzene : isopropanol : distilled water (100 : 12 : 0.25) solvent. The single pigment components were eluated in ethanol (carotenoids) and in acetone (chlorophylls) and the pigment quantities [mg $\cdot$ g^{-1}(dry weight)] were calculated according to the formulas of HAGER and MEYER-BERTENRATH (1966) using the specific absorbance coefficients of the components (HAGER and MEYER-BERTENRATH 1966).

Sampling

The soil samples and the leaves for water relations and photosynthetic pigment determinations were always taken at 7 a. m. It is known that the leaf water content changes with the leaf age (KOZLOWSKI 1964), even the changes of the leaf water content are considerable during one day, too (RYCHNOVSKÁ et al. 1972, KOZLOWSKI 1964). The amounts of the photosynthetic pigments show a daily rhythm as well (HAWKINS et al. 1981). Moreover the leaf samples were taken from the middle parts of the leaves, since the distribution of the pigments changes in the direction from the apex towards the base. However, the leaf samples were chosen from identical leaves, whereby the discrepancies caused by the differences in the ages of the leaves were eliminated, since the quantity and the ratio of the pigments change considerable during the ontogenesis (ŠESTÁK 1977, 1978).

Results and discussion

Soil moisture content

During the wet periods the soil moisture content of the concerned plant community is 11–12%, while during dry periods it is only 2.5–5.5% (Fig. 1). Hence even the water capacity of light sandy soil is little, but the changes of moisture content are considerable and the drying process is rapid. Therefore, by irrigation and natural drying two extremes of soil moisture contents can be produced, and this way the aim of investigation is well supported.

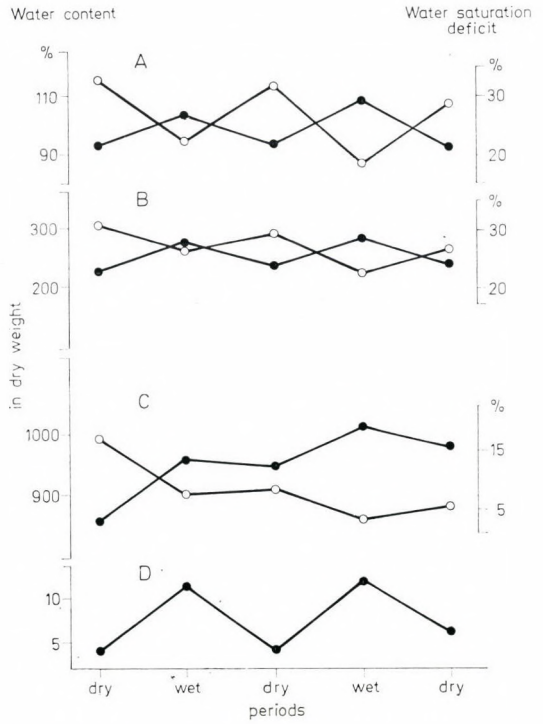

Fig. 1. Changes of the soil (D) and plant water content (●) and water saturation (○) deficit in *Festuca vaginata* (A), *Achillea ochroleuca* (B) and *Sedum sexangulare* (C)

Plant water relations

The schlerophyllous, malacophyllous and succulent character is sensitive regarding the water content values of the leaves belonging to different species (Fig. 1). The water content of the leaves is increasing in all the three species during wet periods, while decreasing during droughts. The change of the water deficit is the greatest in the schlerophyllous *Festuca* and lowest in the succulent *Sedum* (Fig. 1).

The transpiration rates of the three species are lower in the dry than in the wet periods (Table 1). In relation to this the water turnover rate is lower at low soil moisture content than

Table 1

Microclimatic values of Festucetum vaginatae community in subsequent short dry and wet periods

	a	b	c	d	e	f
	°C			%	$\mu E \cdot m^{-2} \cdot sec^{-1}$	
28 07*	39	8	28.4	35	1087	66.6
29**	38	6	27.1	36	1175	72.8
30	39	7	28.0	39	1263	
31	36	9	26.4	37	1157	
01 08	37	10	25.8	40	1035	
02	36	8	27.0	41	1140	
03*	36	7	25.6	38	1245	77.2
04**	35	6	25.0	41	1122	70.2
05	34	5	26.4	40	1288	
06*	35	7	25.7	38	1140	

a = maximal air temperature at 20 cm height
b = minimal air temperature at 20 cm height
c = maximal soil temperature at −5 cm depth
d = minimal air humidity at 20 cm height
e = maximal light intensity at 20 cm height
f = light intensity at sampling time
* dry period
** wet period

at high soil moisture content (dry and wet periods, respectively; Table 1). The increase of soil moisture content induces water uptake and transpiration in an increased degree and as a consequence of this, the water turnover rate increases, too, which leads to the increase of plant metabolic activity. In the case of drought the course is just the opposite as above.

Microclimatic conditions

There was no significant difference between the microclimatic parameters of dry and wet periods (Table 2).

Therefore the changes in pigment composition during the subsequent dry and wet periods should be assigned to the changes in soil and plant water relations.

Table 2

Values of the daily (from 6.00 to 20.00 h) transpiration and water turnover rate of the examined species in dry and wet period

	Transpiration rate $g \cdot g^{-1}$ (dr.w.) $\cdot$ day^{-1}		Water turnover rate $g \cdot g^{-1}$ (H_2) $\cdot$ day^{-1}	
	dry	wet	dry	wet
Festuca vaginata	3.01	7.49	4.70	5.93
Achillea ochroleuca	9.47	15.86	5.88	6.96
Sedum sexangulare	5.01	8.62	0.83	1.02

Carotenoid transformation

Carotene and lutein (+zeaxanthin) content

Carotene and lutein (+zeaxanthin) content of *Festuca* and *Achillea* respond sensitively to the changes of water relations. The carotene content of *Festuca* and *Achillea* increases during dry and decreases during wet periods (Figs 2A and B). The lutein (+zeaxanthin) content decreases during dry periods and increases during wet ones (Figs 2A and B). Quantity of carotene in *Festuca vaginata* is higher than its lutein (+zeaxanthin) content in all the three dry periods. But the carotene content of *Achillea* is lower than its lutein (+zeaxanthin) content both during dry and wet periods. The carotene content of *Sedum sexangulare* increases in the second and third periods, and from the third period on it decreases; its lutein (+zeaxanthin) content increases continually during all periods (Fig. 2C).

Antheraxanthin, violaxanthin and neoxanthin

There are close connections between the changes of water deficit and violaxanthin and antheraxanthin content. *Festuca vaginata* and *Achillea ochroleuca* again behave in a similar way. Among dry conditions the lower amount of violaxanthin is accompanied by a higher amount of antheraxanthin, and vica versa (Figs 3A and B). As a consequence, it should be considered that among drought conditions the deepoxidation of violaxanthin (YAMAMOTO 1979, etc.) into zeaxanthin may be inhibited, and this process favours the accumulation of antheraxanthin.

Table 3

Neoxanthin content (mg $\cdot$ g^{-1}) changes of Festuca vaginata, Achillea ochroleuca and Sedum sexangulare in subsequent dry and wet periods

Periods	*Festuca vaginata*	*Achillea ochroleuca*	*Sedum sexangulare*
dry	0.022	0.054	0.028
wet	0.022	0.067	0.050
dry	0.049	0.105	0.081
wet	0.053	0.121	0.096
dry	0.064	0.135	0.084

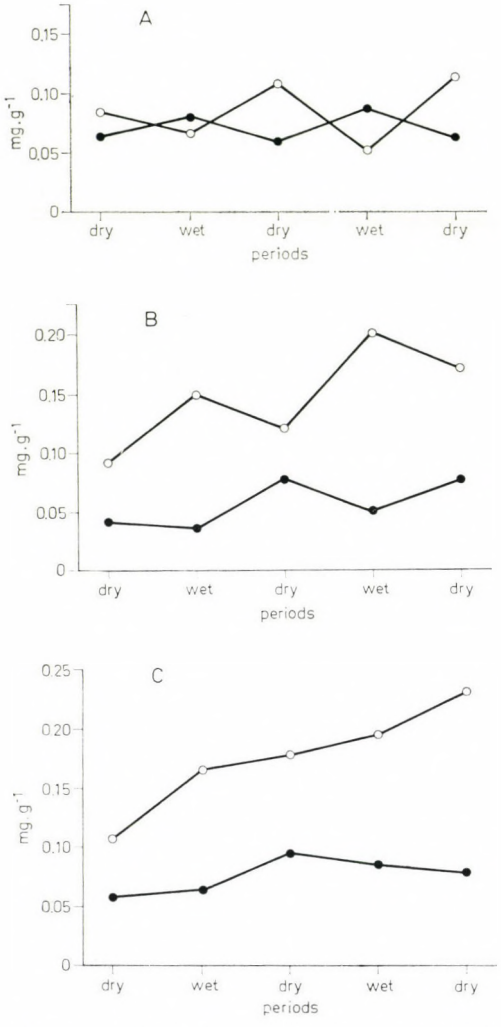

Fig. 2. Transformation of carotenes (•) and lutein (+ zeaxanthin) (○) in *Festuca vaginata* (A), *Achillea ochroleuca* (B) and *Sedum sexangulare* (C) during subsequent short dry and wet periods In the case of *Festuca vaginata* (A) carotenes are indicated by circles and lutein by dots.

Our experience with *Sedum* shows, that due to the carotenoid synthesis induced by the first wet period both the lutein (+zeaxanthin) and antheraxanthin contents increase (Figs 2C and 3C). In this species the change of dry and wet periods effects only the violaxanthin. Its amount decreases during dry and increases during wet periods.

The neoxanthin content of the examined species — except for the first wet period of *Festuca* (no change) and the last period of *Sedum* (only minimal change) — increases period by period. This increase is stronger during dry than during wet periods (Table 2). The fact that the most hydrophilous carotenoid — neoxanthin — accumulates gradually in the drought adapted species during subsequent short dry and wet periods probably plays an important so far unknown role. It is very reasonable that as a component of the light-harvesting CHL

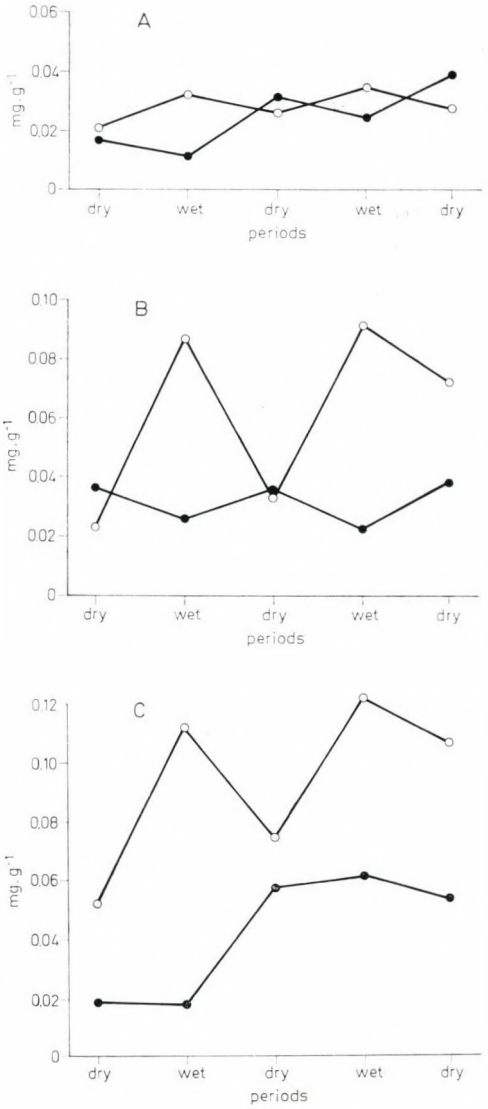

Fig. 3. Antheraxanthin (●) and violaxanthin (○) transformations of *Festuca vaginata* (A), *Achillea ochroleuca* (B) and *Sedum sexangulare* (C) during subsequent dry and wet periods

a/b-protein (THORNBER 1975), neoxanthin takes part in the stabilization of the complex and protects the complex against the destruction.

Pigment ratios and pigment system ratios

The distribution of the chlorophylls and carotenoids within the two pigment systems and the light-harvesting CHL a/b-protein is different and characteristic of each (BRIANTAIS 1967, GROSS et al. 1966, BOARDMAN and ANDERSON 1967, LICHTENTHALER 1969, THORNBER

1975, SIEFERMANN-HARMS 1980). Founded on the different pigment distributions of the two pigment systems and CHL a/b-protein complex, such pigment ratios can be established, which inform on the ratio of the two pigment systems. A ratio of this kind is the generally known chlorophyll a/b one. Obviously, the ratio of the two pigment systems and CHL a/b-protein complex can be given with more certainty if more than one ratio is known. Relying on this, for characterizing the ratio of the pigment systems we have set up new ratios: the ratio of carotenes/chlorophyll b and carotenes/xanthophylls. The higher values of the ratios carotene/chlorophyll b, carotene/xanthophylls and chlorophyll a/chlorophyll b may indicate a higher ratio of pigment system 1 against system 2. On the other hand, a decrease in the ratios

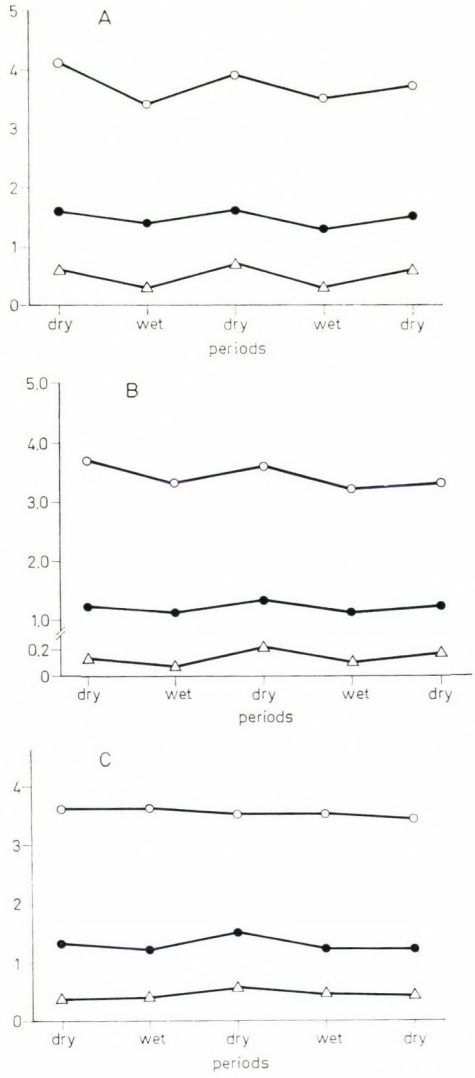

Fig. 4. Changes of chlorophyll a/chlorophyll b(○), carotenes/xanthophylls (●) and carotenes/chlorophyll b (△) ratios in *Festuca vaginata* (A), *Achillea ochroleuca* (B) and *Sedum sexangulare* (C)

rather means the increase of the share of the second pigment system together with the associated light-harvesting CHL a/b-protein (TUBA 1981). As a consequence of the above, among dry conditions the ratio of pigment system 1/pigment system 2 (with the CHL a/b protein) is higher by the examined species, while among wet conditions this ratio will decrease. The same change can be observed on the basis of the ratio of chlorophyll a/chlorophyll b, carotenes/xanthophylls and carotenes/chlorophyll b (Figs 4A and B). These changes of pigment system ratios were the highest in the schlerophyllous *Festuca*, lower, but well defined in *Achillea*, finally only on the basis of carotenes/xanthophylls ratio can be observed in the succulent *Sedum* (Fig. 4C).

Conclusions

During shorter dry periods even the drought adapted species show typical carotenoid (and chlorophyll) transformations due to water shortage. On the basis of our results it can be concluded that in the examined species from the point of view of their different response to water shortage these symptoms are appearent at a different rate. The schlerophyllous *Festuca vaginata* reacts most sharply to the changes in the soil water content, while the response of the malacophyll *Achillea ochroleuca* is less expressed, but well defined and the succulent *Sedum sexangulare* shows a similar reaction only after longer drought. The degree of response decreases with succulency.

In the adaptation to drought we assign importance to the amount of carotenes. Increasing of carotene quantity during stress may have some advantages:

— It may take part in maintaining the integrity of thylakoid membranes. [In the absence of carotenes thylakoid membranes are demaged, but β-carotene reconstitutes the integrity (BASZÝNSKY and TUKENDORF 1975, 1977).]

— Increasing of carotene quantity can increase the activity of pigment system 1 and the activity of cyclic photophosphorylation, which may have a favourable role during water stress. [Adding of β-carotene normalized the decreased activity of cyclic photophosphorylation and photosystem 1 (BASZÝNSKY and TUKENDORF 1975, 1977, TUKENDORF et al. 1980).]

Among wet conditions, due to the effect of better water supply an intensiver carotenoid synthesis is at hand. This increases the lutein (+zeaxanthin) content and the amount of the other epoxyxanthophylls as well. Most striking is the change of the violaxanthin content.

The changes of the chlorophylls [TUBA 1983; which coincide with former records on chlorophyll changes in relation to the changes of water conditions: both chlorophyll a and b concentration is reduced and the chlorophyll a/chlorophyll b ratio is increased during the drought periods (DUYSEN and FREEMAN 1974, 1976, ALBERT and THORNBER 1977, SPYROPOULOS and MAVROMMATIS 1978)] and carotenoids among dry and wet conditions may modify also the ratio

of pigment systems and the CHL a/b-protein complex. These changes in pigment system ratio may strongly influence the ratio among functions connected to pigment systems. By low soil moisture content the schlerophyllous *Festuca vaginata* and malacophyllous *Achillea ochroleuca*, in case of longer drought even the succulent *Sedum sexangulare* seem to possess higher ratio of pigment system 1 to pigment system 2 (and CHL a/b-protein complex). Consequently, it can be supposed that in that case the reactions connected to pigment system 1 are more active, too. The lower water potential reduces the activity of pigment system 2 (VIERIA-DA SILVA and VELTKAMP 1970, FRY 1972, POTTER and BOYER 1973, POSPISILOVA et al. 1976), first of all the electron transfer is reduced that way (KECK and BOYER 1974). Among these conditions the cyclic photophosphorylation connected to photosystem 1 should play an important role in the ATP supply. This view is supported by KECK and BOYER (1974), who considered that the cyclic photophosphorylation proceeds with full activity in the range of -10, -11 bar water deficit.

It is probable that the transformation of the photosynthetic pigments is involved in the adaptation of the photosynthetic system to extreme water ecological conditions.

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Editor: G. FEKETE

C. FEDTKE (ed.): Biochemistry and Physiology of Herbicide Action. SPRINGER-Verlag, Berlin–Heidelberg–New York 1982, 202 pp.

This book provides a very good up-to-date overview of biochemical mechanisms and especially of the physiological aspects of herbicide action. The book discusses in detail the effects of different herbicides on the metabolism of higher plants and as an introduction "intends to promote the future use of herbicides as metabolic inhibitors in plant physiological research".

In accordance with this purpose, the material is divided up into areas of plant metabolism, such as photosynthesis, nucleic acid and protein synthesis, lipid metabolism, and aromatic amino acid biosynthesis.

The first chapter contains a very good concise review on the different approaches to the classification of mechanisms of herbicide action. In order to support the classification and elucidation of the mechanisms of herbicide action, six types of data obtained from different types of observations (application technique, damaged tissue, cytological, physiological, biochemical experimentation, protein/enzyme interactions with herbicides) have been distinguished. Moreover, in order to promote a better understanding of the properties of data from physiological or biochemical systems, terms mechanism, mode and site of herbicide action, as well as basic, intermediate and secondary metabolisms have been explained.

The most comprehensive chapter in the book deals with the physiology and biochemistry of photosynthesis-inhibiting herbicides of different composition and mechanism. In this chapter the action of diuron (DCMU) herbicide and binding at the diuron site have been described in detail. Diuron is one of the best known photosynthesis-inhibiting herbicides, which has been employed as a standard photosynthesis and metabolic inhibitor in many physiological experiments for a long time. The future use of diuron in photosynthesis research has also received special attention in this book. The mechanisms of many herbicides inhibiting at the diuron site and their influence upon different plants have been demonstrated. These herbicides have been grouped into classes containing similar structures : urea derivatives, anilides, s-triazines, s-triazinones, uraciles, bicarbamates, pyridazinones, hydroxybenzonitriles, nitrophenols, benzimidazoles. The structure of each herbicide is shown in tables together water solubilities and pI_{50}-values as obtained in isolated chloroplasts.

Moreover, we can also find many important tables containing the observed physiological effects induced by photosynthesis-inhibiting herbicides. Two molecular mechanisms have been suggested for the interpretation of the so-called "physiological effects": 1. regulatory responses caused by a low photosynthetic rate and a decreased carbohydrate production in the herbicide-treated plants, and 2. hormone-like effects, e.g. growth stimulation.

Other parts deal with the role of herbicides in the electron transport, the inhibition of photosynthetic pigment systems I and II, and the carotenoid biosynthesis.

Two chapters are devoted to the herbicides interfering with auxin activity. The microtubules occurring during cell division in higher plants, the microtubular systems influenced by herbicides, and other morphological and cytological effects induced by herbicides are also discussed in the book.

There is a good review on the plant lipid mechanisms induced by different herbicides. A possible mode of herbicide action has been presented and the effects of thiolcarbamate herbicides on the inhibition of germination and the interference of these herbicides with photosynthetic and respiratory systems are emphasized.

In summary, this book provides an adequate and up-to-date coverage of the various modes of herbicide action and is recommended to all researchers dealing with herbicides and all physiologists.

The layout of this book with 43 figures and 58 tables is fine. References are found at the end of each chapter and a subject index is also included.

K. VIRÁGH

F. LENCI and G. COLOMBETTI (eds): Photoreception and Sensory Transduction in Aneural Organisms. Plenum Press, New York and London 1980, 422 pp.

This volume includes all the lectures presented during the Nato Advanced Study Institute Conference on "Photoreception and Sensory Transduction in Aneural Organisms" held in Villa Le Pianore (Versilia, Italy), September 3–14, 1979.

The greatest merit of the book is the "interdisciplinary approach to the problem of photoreception and photosensory physiology in aneural organisms, bringing together scientists from different fields and specializations". Moreover, it has brought the different photobiological sciences closer at a higher interdisciplinary level.

The essential problems and the new results of photoreception and sensory transduction are discussed. The most important research results are summarized with a forecast of the unsolved problems to come into prominence in the future. The volume includes twenty-two studies.

The introductory study surveys the sensory transduction (orthokinesis, temporal and spatial sensing, adaptation, interactions, types of stimuli) in aneural organisms (bacteria algae, protozoa and fungi).

In the second study a detailed picture of the physical properties of the light beam is presented.

The following four studies deal with photometile responses in Flagellates (*Euglena*, *Volvox* and *Chlamydomonas*), gliding organisms and bacteria, phototropism of lower plants (algae, *Phycomyces*, *Dryopteris*, liverwort and moss) and the experimental determination and measurement of photoresponses.

The following three studies deal with photoreceptive apparatus of flagellated algae cells, the localization and orientation of photoreceptor pigments (chlorophyll, carotenoids, phycobilins, bacteriorhodopsin, stentorin) and their identification and spectroscopic characterization. Their main theme centers around the question of comparative apparatus (type I–IV), their function (trajectory control, sensor, photopigment turnover, feedback canal and effector), localization and orientation of photoreceptor pigments in *Halobacterium halobium*, *Mougeotia* spec., *Phycomyces* sporangiophore and *Euglena gracilis* and analysis of the action spectra in photomovements.

In the study: "Primary photophysical and photochemical reactions: theoretical background and general introduction" the photoreactivity of flavoprotein is in the centre of focus beside the description of carotenoprotein analysis.

In the following three studies the molecular aspects of photoreceptor functions are dealt with. The photophysical and photochemical properties of carotenoids and rhodopsin are the main concern of the study of R. V. BENSASSON.

In the Pill-Soon Song's study the author presents a description of a model for the physiologically active form of phytochrome. The study entitled "Molecular aspects of photoreceptor function in *Stentor coeruleus*" includes the characterization of photoreceptor (chromophore structure and subunit organization of the protein) and the proposed primary mechanism of the *Stentor* photoreceptor (proton flux event).

In the subsequent two studies a detailed theoretical picture is presented of the photoregulation by flavoproteins, bluelight reception and flavin phytochemistry.

The following study deals with the basic concepts of bioenergetics, such as the GIBB's free energy, flows and forces in irreversible processes, coupling between flow mass and chemical reactions (primary and secondary transport) and ATP synthesis coupled to redox reactions, respectively. J. AMESZ's study is a good summary of the photosynthetic membrane properties: primary reactions, secondary electron transport, pigment-protein complexes and electrochromism.

The four last studies deal with structural and functional aspects of photoreception in lower and higher organism, photosensory transduction chain in Eucaryotes and Procaryotes, and sensory transduction in phototropism (genetic and physiological analyses in *Phycomyces*).

The closing study of the volume is a panel discussion: "Sensory transduction and photobehaviors: final considerations and emerging themes" presented by W. HAUPT.

Well selected and abundant references are given at the end of all the studies.

The compilation of the whole volume testifies to F. LENCI's and G. COLOMBETTI's (Consiglio Nazionale delle Ricerche Pisa, Italy) excellent editorial work. The book's typographical layout is also to be praised. It can be highly recommended to research workers and to students as well.

Z. TUBA

J. REINERT and M. M. YEOMAN: Plant Cell and Tissue Culture (A laboratory manual). SPRINGER, Berlin, Heidelberg, New York 1982. DM 49.50

The totipotency of plant cells hypothesized early this century has not only been proved by the application of tissue culture but used directly and indirectly in the horticultural, agricultural, sylvicultural and industrial practice. On the one hand plant tissue culture promotes the study of the induced, reproducible and regulable development of uncorrelated plant parts (pollen, cell, protoplast, tissue, organ, embryo). On the other hand, otherwise unaccomplishable experiments with regeneration, hybridization, cell transformation, genom preservation, suppression of pathogens, resistence induction, and in genetics, plant breeding and propagation, and fermentation industry, etc., are facilitated.

The success of such experiments is conditioned upon a profound knowledge of biological principles, technical experience and manual skill. The necessary information is available in proceedings and general manuals. Laboratory technology, however, is most rapidly and easily acquired from analytical handbooks with sufficient repetitions. The latter purpose is aimed at in this manual. The authors are noted representatives of the field, being writers, co-authors or editors of several publications concerned with the theory and application of plant tissue culture.

The 83-page manual contains 37 figures, mainly line drawings. The introductory part outlines the purpose, use and presentation of the book. Then, seven chapters follow. The first describes the isolation of plant inoculae, the mechanism of their growth and cell division, subcultures, production of cell suspensions and the dynamics of individual cell growth using *Daucus* and *Helianthus tuberosus* objects in four experiments. Chapter 2 evaluates the growth response of tobacco and soybean tissues to a treatment with cytokinin. The third part shows the regeneration based morphogenesis in four experiments: the embryogenesis of *Daucus*, the (haploid) embryogenesis of *Nicotiana* callus and anther cultures, and the vegetative propagation of *Cymbidium* using protocorms. Chapter 4 describes the isolation and fusion (with PEG) of tobacco leaf protoplasts in two experiments. Other two experiments in the next chapter serve as an evidence for the synthesis capacity of secondary metabolites, anthocyanin (*Haplopappus*) and diosgenin (*Dioscorea*), of callus tissues. The three experiments of chapter 6 exemplify the development of *Zea* embryo, and the organization of *Pisum* roots and *Dianthus* shoots. Finally, an Appendix lists important handbooks, laboratory instruments, materials and their suppliers. Afterwards, the determination of cell mass and cell number is described, different methods of sterilization and glass cleaning are presented. Recipes of stock solutions most efficient in different cultures (embryo, anther, etc., and *Daucus*, *Nicotiana*, etc.) are given. The manual is supplemented with an authors' index and a subject index.

As demonstrated above, this book comprehends almost all fundamental aspects and model objects of plant tissue culture. The description of the things to do in each experiment is straightforward, the tasks are essentially simple, precise and reproducable. The execution of each experiment is facilitated by a definite list of materials, instruments and tools. The jobs are described in detail and the time necessary to obtain a final result is also indicated. The step-by-step description of experiments and the schematic drawings of setups are also of great help. Repeated execution of experiments is suggested in order to yield acceptable results. The authors also propose to record the observations in a notebook and to raise questions concerning the basic principles and applicability of experiments. Although the latter suggestions appear to meet didactic requirements of graduate studies, they are necessary to a successful completion of experiments.

Summing up what has been said, I think this manual is an important and valuable contribution to the practice of tissue culture. The excellent design is customary to SPRINGER, which is further improved by P. Macdonald's expressive line drawings. The book is strongly recommended primarily for educational purposes of university courses but also for researchers.

M. MARÓTI

F. JACOB–E. J. JÄGER–E. OHMANN: Kompendium der Botanik. VEB Gustav FISCHER Verlag, Jena 1981, 494 pp.

The reader may get acquainted with the Compendium of Botany, Botanic Handbook, which is one of the new members of the general handbooks (compendia) published so far in the GDR, written by the well-known authors, F. JACOB plant-physiologist and microbiologist, E. J. JÄGER botanist and plant-geographer and E. OHMANN plant physiologist and microbiologist.

As the book encompasses a wide botany, its structure differs from those wellknown up to now. It has been intended to be a text book for biologists, biochemists and biology teachers in training and an accompanying, complementary text book for pharmaceutical workers, chemists and students studying agriculture.

In the first part of the book the principle of the development of plant life is described and a place is assigned to the plant in the energy regime of nature and a short description is given of the main parts of botany as a summary branch of science.

In the second part, the structure of the plants, their elementary composition and the role of the individual chemical elements are described with the so-called metal enzymes also being summarized. The role of water and the biological macromolecules is discussed and a detailed description is given of nucleic acids. The part that proteins and amino-acids, carbohydrates and lipids play in the plant metabolism are dealt with in separate subchapters.

In the third part a detailed survey is given of the plant cell, the role and material of the nucleus, plastids, mitochondrium, cytoplasm, paraplasmatic structures, with their formation and importance being also given. In a summary of this theme the "cell" of the so-called procariots (bacteria) is presented.

Chapter four treats the plant tissues on the basis of their classical classification.

Chapter five deals with the "real" plants, describing their basic organs. (Its subchapters are: Seed and juvenile plant; sprout top — from its formation to its stabilization — describing its individual parts, such as the leaf, root.) The form and change in function of the basic plant organs as well as the spread and propagation of the plants can be found in a separate subchapter.

In chapter six plant taxonomy and evolution are described. This chapter of some 130 pages can give only a narrow survey of the material of the systematization, which is complicated and can be interpreted in various ways, and the results of which have been discussed in part here and there. A survey is given of the bases of plant systematization, with its task, development and methods being described and an inside view is offered of the taxonomic categories and the science of taxonomical names, respectively.

In the subchapter on research of evolution, plant inheritance is referred to, and just here a short survey can be obtained of the plant taxonomy (from the procariots to the best developed flowering plants). It is a pity that this page illustrated by some 120 figures can give only a little inside view of the system of the whole plant world, although the recent results of the related branches of knowledge are also treated in it. The figures facilitate comprehension of this large material according to recent viewpoints.

In chapter seven the plant metabolic physiology is described and the most important and fundamental information obtained from the researches of plant nutrition are summarized by using the recent results of research. The most important biochemical processes taking part in the building up and decomposition of the plants are described on the basis of the bioenergetics of metabolism, with the types of metabolism being also classified in detail. The water regime and the role, intake transportation, so-called cycles of the most important mineral elements are described in separate subchapters. The formation and the importance of the so-called secondary metabolic products are made known and the types of heterotrophic nourishment are classified. In this chapter a picture is given of the realization of the genetic information.

In chapter eight dealing with development physiology, the growth of the plants, the genetic background, regulation and processes of the differentiation are detailed. The plant hormones playing a part in the development of the plants, the phases of the plant organ formation, its biochemical bases including the photoperiod, the plant sensitivity and the rhythms of the plant life are described in separate subchapters.

In chapter nine dealing with kinetic physiology a survey is given of the most important motions to be found both in primitive plants and in those of high development. The motions caused by the external factors (e.g. sensitivity, tropism, nastia, taxis, etc.) are described in separate subchapters.

Having described these most important areas of botany, the authors give a detailed bibliography for furthering our plant taxonomic knowledge.

The book does not treat the details of plant inheritance, the themes of plant geography, paleobotany and ecology which are also closely related to botany. But the authors indicate that the forthcoming summary handbooks (Kompendium der Genetik, Kompendium der Ökologie) will deal with these themes in detail. This fact also shows that in the far-reaching themes of botany those which have been omitted have recently been developing so much that a separate book on each would be necessary.

The book entitled "Kompendium der Botanik" is, so to say, a moderate compromise for a clear covering of the most up-to-date and conventional knowledge. The brief special text is supplemented with many figures, pictures, and tables, of high standard, easy to look over and facilitating easy comprehension of the text. Each part is taken from other handbooks and text books, which are correctly indicated by the authors.

The book is written in a lucid, simple style, and to the point and it is easy to understand for those who are poor in German.

The value of the book is raised by the special subject index terms register to be found at the end of the book. In 1981 the book "Kompendium der Botanik" was accepted as a text book for higher education by the tertiary education ministry in the GDR.

The lay out of the book is simply beautiful but practical.

P. KLINCSEK

H. GERMAIN: Flore des Diatomées, Diatomophycées eaux douces et saumâtres du Massif Armoricain et des contrées voisines d'Europe occidentale. Société Nouvelle des Éditions Boubée, Paris 1981, 444 pp.

The book of Germain is a new part of the volumes Collection "Faunes et flores actuelles" of the publishing company. The previous books of the series, such as the three-volume "Les algues d'eau douce" by P. BOURRELLY or the two-volume "Les Copépodes" by B. DUSSART are world famous. The book written by GERMAIN on the diatoms can be rightly ranged with these. The internationally well-known algologist summarizes the researches of some 50 years in this work.

In the Introduction following the short Preface, the Author describes the collection and preparation of diatoms as well as how to examine them under the microscope and how to use the taxonomic keys; a list is given of some important comprehensive books on diatoms.

In the following chapter the general characteristics of the diatoms, the frustule-structure of the *Centrophycidae* and *Pennatophycidae* sub-classes, and the basic morphologic features of the frustule are presented accompanied by drawing. This chapter of a few pages would have deserved a more detailed description.

A systematic part follows over 375 pages. The Author essentially follows HUSTEDT's system (RABENHORST' Kryptogamenflora 1927–1963). He mentions that SIMENSEN's (1979) new diatom systematization became known to him only after having finished his own book and so he could take only a fraction of SIMENSEN's systematization into consideration.

In his book GERMAIN divides the described diatom species into the following groups:

Subclass:	*Centrophycidae*	
Order:	*Coscinodiscales*	28 species
	Rhizosoleniales	1 species
	Biddulphiales	1 species
Subclass:	*Pennatophycidae*	
Order:	*Diatomales* or *Fragillariales* or *Araphidae*	29 species
	Eunotiales or *Brachyraphidae*	19 species
	Achnantales or *Monoraphidae*	28 species
	Naviculales or *Biraphidae*	351 species

Thus altogether 457 species are desribed. Within the species the Author often describes variants and forms, too. In addition to this, valuable ecologic data are also given for most of the species.

H. GERMAIN undertook a difficult task when he wrote a book on the diatom flora of the studied area, which, apart from the description and characterization of the species, also

includes taxonomic keys. The dichotomic taxonomic key of the species is based on the morphology of the diatom frustule. The microstructure elements to be studied by light microscope can also be found in the taxonomic keys. The description of the taxons is complemented by an extremely rich microphoto material, facilitating the determination. Of these 2 005 have been made by light microscope, 120 by transmission electromicroscope, scanning electronmicroscope. It is a pioneer effort that the knowledge and accurate determination of the species are facilitated by microphotos instead of drawings.

The book deserves appreciation because it is built on a wide range of investigation materials, is extremely well illustrated and includes valuable ecological data on most of the species.

It would have only gained in worth drawings had been added to the microphotos in the small-sized alga. In this way the description and diagnosis of each species could have been revealed in more details (e.g. the *Cyclotella cryptica*). That does not detract from the merit of his work. H. GERMAIN's book can be recommended for all diatom-specialists, algologists, botanists and hydrobiologists. The book can be recommended to all those who want to be given a basis, apart from the strictly-spoken taxonomic knowledge, for the practical points of view of water qualification, and to know the conditions of water halobity, trophity, saprobity by studying of the diatoms.

K. T. KISS

S. ORBÁN–L. VAJDA: Magyarország mohaflórájának kézikönyve (Handbook of the Hungarian Bryoflora), in Hungarian. Akadémiai Kiadó, Budapest 1983, 518 pp., 19 photos + 588 line drawings. ISBN 963 05 2889 4. Price in Hungary: Ft 160.—

The long wanted book was issued right 30 years after the publication of the first comprehensive Hungarian bryoflora (Magyarország mohái — Bryophyta Hungariae by Á. BOROS, 1953, Akadémiai Kiadó, 360 pp.). Although BOROS' book was very useful in his time and promoted bryological activity in Hungary, during the last decades became out of date, partly due his old nomenclature, partly the many new discoveries in Hungarian bryoflora. Therefore the two experts of our bryophytes met real demands, when decided to write a new, up to date manual of our bryoflora. Hungary is not rich in bryophytes, being a country with semihumide and in its greater part with semiaride climate, but even so is an interesting crossway of northern temperate, continental and mediterranean geographical elements. Therefore the Manual, even written in Hungarian, might proved to be useful for the foreigner scholar, accumulating all taxonomic, phytogeographical and ecological knowledge on the bryophyte species occurring here.

The book is divided into three chapters. The first one includes the history of Hungarian Bryology, the most important morphological, phytogeographical and ecological features of bryophytes. It contains useful and detailed informations about the collecting and storing of bryophyte specimens, and gives short guidence to the further bryological research and its methodology (cytotaxonomy, cultures, etc.).

The second chapter enumerates the most important manuals on European bryoflora. The further publication list contains only additions to the detailed bibliography in BOROS' other book (Bryogeographie und Bryoflora Ungarns, Akadémiai Kiadó 1968, 466 pp.).

The third and main chapter (pages 61–501) covers the detailed determinatory and descriptive part of the book. It includes generic and specific keys (and in addition, original family keys for *Musci*). Almost all species descriptions are accompanied by figures. Most of the line drawings were made under the Authors' auspices by Mrs. L. BUCSI — when not original, indicated in the legend. The tables with these figures are incorporated among the text pages. The only disadvantage experienced by the figures is, that no direct reference by the species description to the concerned figure — this can be found by the user in the Index on pages 507–518, with indication of the table and figure numbers.

In the text, after the species description finds reader reference to the ecology of the species, first of all to its substrate, then the Hungarian distribution is enumerated, by more widespread species according to large geographic units, by rare elements in details. Finally the phytocenological taxa are enumerated, — in which plant communities occur the concerned species.

The manuscript was submitted already in 1979. Due to delayed printing several recent discoveries and nomenclatural changes could not be incorporated in the main text, therefore these are enumerated on pages 502–506.

The book is hardbound, typographycally clear and easy to handle. Surely, it will encourage students and amateurs to deal with bryology, also will help stimulate the work of

trained bryologists both inland and abroad. We would like to congratulate the Authors fulfilling this very laborious task.

G. Kis

R. Moberg: The Lichen Genus Physcia and Allied Genera in Fennoscandia. Acta Universitatis Upsaliensis, Almquist and Wiksell International, Stockholm–New York 1977, 108 pp., 42 figures and 26 maps

No doubt that *Physciaceae* is one of the most intensively studied lichen family. Refer to, for example, Sántha (1928) or L. Gallé's work which remains incomplete due to his death. Despite the popularity of this family, a book using modern methods and discussing the ultrastructure, morphology and the chemical characteristics of species was badly needed. Moberg's monograph seems to fulfill this need.

The book gives an account of a thorough examination of 20 000 herbarium specimens of lichens. The author himself did regular collecting trips to Sweden, Norway, Finland and Denmark.

Modern techniques, such as electron microscopy, scanning electron microscopy and thin layer chromatography are used and a new genus, *Phaeophyscia*, is described. This work represents an example that cytological characteristics, even when new genera are distinguished, and histology are more and more emphasized in contemporary lichen systematics.

Another virtue of the book is that taxonomic units are treated with caution. Interesting varieties are introduced, e.g., in case of *Physconia pulverulenta* and *Physcia stellaris*.

Detailed taxonomic description and ecological characterization are given for 30 taxa. Most of them occur in Central Europe as well. Thus, this monograph is also useful in Hungary and the neighbouring countries. The maps showing the geographic distribution of taxa are precisely and neatly drawn.

The extensive bibliography contains 157 items, including Sántha's paper.

The excellent figures and the good identification key may be useful for both the advanced lichenologist and the beginner.

T. Kiss

S. J. Casper–H. D. Krausch: Pteridophyta und Anthophyta. 2 Teil: Saururaceae bis Asteraceae. VEB Gustav Fischer Verlag, Jena 1981. pp. 404–942, 119 Tables, 1695 figures. The book is published as Volume 24 of the series "Süßwasserflora von Mitteleuropa" (hrsg. H. Ettl–J. Gerloff–H. Heynig)

The book is a continuation of the first part issued in the same series (Volume 23, *Lycopodiaceae* bis *Orchideaceae*).

In this second volume species are described which can be found in the waters and soggy, wet habitats of Central Europe. The native and introduced plant species are equally described in the identification hand-book.

Three kinds of taxonomic keys can be found in the first part of the book. The first one is based mostly on generative criteria and serves to determine the families and main groups. By means of the second taxonomic key mainly the populations (and partly the species) can be identified, relying on the properties, criteria to be recognised easily. The third taxonomic key serves the determination of the plants submerging in water.

In the special part more than 300 species and several subspecies are described in detail. The morphological characteristics and area geographic conditions of the individual populations and species are given. From the description of the species data can be obtained on the chromosome number, flowering period, presence as well as on the ecological and cenological conditions. The extremely rich bibliography includes some 1500 works.

At the end of the book addenda and supplements as well as the author index and species register can be found.

The results of the new researches mainly those of taxonomy, area geography and ecology, connected with water plants have been included in both volumes. Providing plenty of information it is an essential identification hand-book for botanists, hydrobiologists, limnologists and ecologists. As a considerable part of water plants can be used as a biological indicator of water contamination and water quality, this book can also be used with advantage by experts dealing with environmental protection.

M. Kovács

P. MÜLLER: Biogeographie. Verlag Eugen ULMER, Stuttgart 1980. 414 pp., 106 figures and 77 tables

The book was published as a part of the well-known and popular series "UNI-Taschenbücher", under No. 731 and is a preliminary, abridged edition of the Author's work entitled "Arealsysteme und Biogeographie" (1981, 704 pp.).

The Author, who is the Head of the Biogeographic Institute of Saarbrücken University, sets forth that the book written for university students is the first attempt to bring biological and geo-sciences nearer to each other. The alarming problems of environmental protection of our age cannot be solved without elementary biogeographic knowledge.

The book consists of the following six main chapters:

Chapter 1. In the framework of biogeography — aims of research and history — the author determines the notion of biogeography and offers a survey of the history of this field of science, from THEOPRASTOS to our days.

In Chapter 2 entitled "Biosphere" a description is given of the essential conditions of the living systems and their constraints the production conditions of the vegetation zones of the Earth, the quantity of annual carbon fixation, the chemical composition of the atmosphere, and the role that oxygen and temperature played in the living systems.

A good description is given for the reader on the genetic macrostructure of the biosphere, the so-called bio-zones of the Earth. We can get acquainted with the floristic and faunal characteristics of the individual bio-zones (Holarctic, Paleotropis, Australis, Neotropis, Archinotis).

In Chapter 3 the area systems as well as the cosmopolitan species and those of small areas are described. The area structure is determined by the genetic differentiation of the populations. Change in the population genetic structure may cause the expansion or regression of the area. From the point of view of the living world, it is of the utmost importance to know the total range of the plant and animal species and to fix the changes taking place.

In the framework of the organs and populations being fixed to space, the Author describes the spatial expansion of the ecosystems, their loadability, stability and regeneration capacity.

In Chapter 4, the connection of the area systems and ecosystems is described, making known the structure, function and loadability of the most important ecosystem types (lake, bog, river, town). The motion of the urban ecosystem is expounded in detail and the ecologic structure of the town, the peculiar climatic and air contamination conditions are revealed. A survey is given of the plant and animal world of the cities as well as their utilization in biological indication, evaluation of the environmental conditions, furthermore of the green areas, woods and their part played in developing a more wealthy urban environment.

In Chapter 5 the biome are presented and there is a detailed description of the life-communities of the individual climatic and vegetation zones to be determined physiognomically, such as the tropic rain-forest, savanna, steppe, desert, evergreen sclerophyllous forest, deciduous forest, boreal coniferous wood, tundra, as well as the high-altitude and seaside communities. The climatic and soil conditions of the individual climatic zones, the characteristic plant and animal species are also described. The chemical and physical characteristics of the sea-biomes, the living world of the sea, the ecologic macrostructure and the production conditions are given in detail.

In Chapter 6 the evolution of the area systems and landscape history are described and of the paleontologic, climatic and Earth historical (glacial periods) and geologic (continuity and shifting of continents) conditions which exerted a great influence on the area geography of the plant and animal species. A survey is given of the separated ecosystems of the isles, illustrated with examples, such as the living world of the South Sea Islands (Krakatou, Hawaii, Galapagos, etc.). The prevalence centres and refuge areas are also described.

The book, providing plenty of illustration material, is complemented with a rich bibliography and special register.

The book is an up-to-date work, taking the results of the new research into consideration. It is not only a university school-book but is a useful work of biogeography, providing appropriate basic knowledge for botanists, ecologists as well as for the experts dealing with environment and nature protection.

M. KOVÁCS

R. SCHUBERT: Pflanzengeographie. 2. bearbeitete Auflage. Akademie-Verlag, Berlin 1979, 307 pp., 78 Abb.

Prof. SCHUBERT's book, published in the second revised edition is an excellent plant-geographical work, in which the vegetation of the Earth is elaborated. The work consists of two main parts. The first part is the plant-geographical (geobotanical) one, its title being identical with the main heading of the book while the second one deals with the vegetation of the Earth.

The plant-geographical part includes the floristic, historical-genetic and ecological plant-geographical parts.

In the part including the floristic plant-geography the Author deals with the role, magnitude and form of the areas and their part played in the flora division of the Earth. The flora division of the Earth as well as a further detailed division of the six flora regions are given too, considering new points of view,.

The historical-genetic plant-geography includes the biogenetic bases of the diversity of the plants from era to era, from the carboniferous period to the tertiary period, in the tertiary period, Pleistocene, in the late and post-glacial periods and during the period of human history.

The ecologica l plant-geography gives an analysis on the diversity of the plants depending on the climate and soil conditions. One of the most valuable parts of the whole work is the growth and life-form analysis elaborating very detailed new points of view as well.

In the part dealing with the vegetation of the Earth first the tropic rain-forests are described. The climatic and edaphic conditions, the architecture of the rain-forests, their zonation according to height, and the agricultural areas, stands forming in their place are made known. Then the vegetation zone of the periodically dry, tropic monsoon forests, the zones of dry forests, thorn-bushes and savannas, the subtropic semi-deserts and deserts and the sclerophyllous and deciduous forest vegetation of temperate zone are described. A separate chapter deals with the semi-deserts, and deserts of temperate zone and the dry steppes. After describing the Northern pine-woods of thc temperate zone, the book ends with the presentation of the tundra vegetation of the arctic zone.

The carefully compiled book of good typographical get-up is illustrated by useful and matterful figures and photos.

Besides the scholars of plant-geography, the book may also reckon with the interest of the biologists, moreover that of the geographers.

Z. TUBA

P. POISSONET–F. ROMANE–M. A. AUSTIN, E. van der MAAREL–W. SCHMIDT (eds): Vegetation Dynamics in Grasslands, Heathlands and Mediterranean Ligneous Formations. JUNK Publishers, The Hague–Boston–London 1981, x + 286 pp. Advances in Vegetation Science Vol. 4.

This volume contains most of the contributions presented at the Symposium of the Working Groups for Succession research on permanent plots, and Data-processing in phytosociology of the International Society for Vegetation Science, held at Montpellier, France, September 1980.

The approx. 70 lectures and poster contributions were arranged around five themes:

I. Succession: theory and methods,
II. Succession in mediterranean ligneous formation,
III. Succession in heathlands,
IV. Succession in herb formations,
V. Succession in dunes, marches, seaside.

The 27 elaborated papers presented in this book represent a broad scale of variation both in topic and locality of the study-site.

One may find reports of succession of mediterranean vegetation on Corse, Balkan, Tunesia, Western Australia, Hawaii, France, etc.

The heathland-studies were located at Bretagne, in Ardennes, Scotland, Balkan and other sites.

As for the theoretical aspect of succession-research there is a growing interest toward spatial heterogenity and related problems. Many authors regard the permanent plots as a point of contact between the temporal and spatial-oriented aspect of succession. They stress that the artificial separation of this two views can not be maintained any longer. It is surprising, how vivid and detailed picture can be drawn on the base of the observation of a

permanent quadrat of many years (e.g. L. ORLOCI presented a time series-study of as long as 40 years).

Several papers are devoted to the conservation problems, as a special branch of succession-studies. The National Parks and other reserved areas should be maintained in their present stage, but the succession sometimes "destroys" what we try to reserve. In many areas we have to face the problem weather we should totally exclude any grazing, pasture-management and hay-making, or not.

An other cluster of problems is the effect of cutting, grazing and different kinds of fertilizers on the floristic composition, production and overall succession of grasslands.

The fire, both natural and artificial, is also a very strong factor in the course of succession and plays a very important role especially in mediterranean shrub vegetation and heathlands. Several papers give an account on this role in France and Scotland.

On one had, it is delightful to see the variety of topics and sites centered around the problems of vegetational succession, but on the other hand, as for the methods used, one may feel confused. Even for the same purpose, e.g. the description of change of permanent plots during the time, there is no consent on the most effective. Therefore, it is very difficult to compare the different results or descriptions.

There is an even more serious insufficiency, the lack of a basic theory, or at least the core of it, of succession. One can find brilliant papers presenting the observations on the "phenology" of succession, but very weak and faint ideas about the explanation of the observed phenomena and poor justification of these ideas or no proof at all.

But these are the general weaknesses of ecology and this volume only reflects where we are.

The book is well-documented and of the usual high standard as the other Junk-publications. It may be highly recommended to whom who are interested in vegetational succession.

Z. Szőcs

L. van der PIJL: Principles of Dispersal in Higher Plants. SPRINGER, Berlin 1982, 215 pp.

With respect to the dispersal of higher plants and the background condition system restricting it the localization and motion of the populations in some kind of suitable topology are in the centre of the interest.

But as to what population characteristics stand behind the speed constants of these motions are hardly considered. The versions of the mechanism of dispersal belong to these properties. The above statement does not mean that there are no works showing the varied possibilities of the plant dispersal. But these are rarely used to interpret the phenobiological events. The Dutch professor has made a step forward in this direction by not only undertaking a summarized systematization of the individual dispersal types but also by trying to find a connection with other scopes of themes, where the individual types have a function.

The book consists of the following main structural units:

1. Part of dispersal in the life chain, the history of the scope of themes, factors limiting the development.

2. Terminological chapter. Here the inconsistencies of the individual terminological systems and the chaos prevailing in this theme are discussed in detail. It is a pity that, besides the criticism, no new system is given, only a simple one is adapted and modified a little but not attempt is made to base this on the things discussed in further chapters (e.g. function — see strategies, biocenosis, evolution). His choice is supported in some way by the fact that he would like to take results in certain inconsistencies and petty compromises.

3. In the following the conncetion between the flower and fruit is analysed, based on the morphology but it is stated that morphology is nothing else but "petrified ecology".

4. Then the individual dispersal mechanisms are dealt with in detail and systematized on the basis of the dispersal agents, with the chosen categories being treated, in spite of their relative rigidness in a rather enjoyable, readable way, and with many tropic examples being added.

5. Dispersal as a strategy and the connection between the biocenoses. Here a rather interesting statement is made on the coordinated character of dispersal but, unfortunately, in a large scale, and only the individual formations are compared on the basis of the spectrum of the dispersal mechanism.

6. A separate but rather short chapter is devoted to the connection between the diaspores, the dispersing agents and fixation as well as the germination.

7. The evolution relations are described in several chapters and the connections between the dispersal, dormancy, sexual motility, sexual differentiation functions are emphasized, and the phylogenetic development of these functions and the organs carrying these functions are analysed in detail. A good example is given for this in the following two chapters where a magnificant analysis is given of the papilionaceae and the grasses. These chapters are the parts of the book which have been most carefully elaborated. It is a particular virtue of the book that the individual diaspore properties, which have been found only as taxonomic stamps, have been interpreted here, and the coevolutions of the stamps and dispersing agents can be followed from the beginning to the end under the changeable environmental conditions of the history of the Earth.

8. The book ends with a short chapter, which deals with the role of man and culture as a dispersing agent. The book was intended to be a textbook. It can be stated that it is a rather valuable, didactic reading accompanied with many beautiful illustrations. It is not only a book for professionals, but because of its anecdotal, lucid style it can be recommended to all those who are interested in the theme. The present third issue differs from the previous one in that the stress has shifted towards the ecologic and evolutionary chapters. The classical work of "natural history" is a part of an enterprise, consisting of several books (see: FAEGRI–PIJL: The principles of pollination ecology) and covers interconnections of great space and time scale. An interesting and valuable continuation of this work could be a work aiming at the interpretation and quantification of the small-scale, phenomena, "within populations".

S. BARTHA–F. HORVÁTH

K. C. MARSHALL (ed.): Advances in Microbial Ecology. Volume 6. Plenum Press, New York and London 1982, 240 pp.

The series Advances in Microbial Ecology presents the latest research on the roles of microorganisms in natural ecosystem. Volume 6 is mainly concerned with the ecology of aquatic microorganisms (bacteria and algae). Contributors examine the role of microorganisms in the cycling of selenium, discuss the effects of environmental limiting factors on phytoplankton growth, review the problems in assessing biomass and metabolic activity of heterotrophic bacteria and their survival in nutrient-deficient marine ecosystems and analyse the role of solid surfaces in the ecology of aquatic bacteria.

Chapter 1. J. W. DORAN: Microorganisms and the biological cycling of selenium. Selenium, an element that is both essential and toxic to warm-blooded animals and certain microorganisms, is cycled predominantly via biological pathways. The study dealing with environmental distribution, microbial transformations and biological cycling of selenium has collected and synthetized the studies carried out on the subject.

Chapter 2. G. Y. RHEE: Effects of environmental factors and their interactions on phytoplankton growth. Factors influencing the primary productivity of phytoplankton have received increasing attention during the past two decades. Sometimes it is not difficult to identify the key factor controlling primary productivity but quite frequently, it takes laborious efforts to discern the responsible environmental stress due to the simultaneous action of more than one factor. Species also differ in their responses to environmental changes. The chapter examines the effects of three principal factors (nutrients, light and temperature) and their interactions in phytoplankton growth. Concerning nutrient limitation the author discusses the functions among phytoplankton growth and nutrient uptake, the question of optimum N : P ratio and multinutrient limitation. Light- and temperature effect on phytoplankton growth, mechanism of light-adaptation, photoinhibition and the interactions with nutrient limitation are analyzed including some biochemical aspects as well. Sporadic records synthetized in the study as well as the author's own results extend our knowledge on the difficult question of niche partitioning among algae.

Chapter 3. H. W. PEARL: Factors limiting productivity of freshwater ecosystems. Despite the high level of apparent physical and chemical uniformity of surface water bodies, a high diversity of microorganisms, all exhibiting distinctly different growth requirements, can exist. How is this possible ? This question is central one in limnology since HUTCHINSON propounded his plankton paradox and the author has also focused on this in this chapter. Geological, physical, chemical and biological characterisics of freshwater ecosystems in relation to nutrient limitation are detailed with special attention to nitrogen, phosphorus, silicon and minor trace elements (iron, manganese, copper, zinc, molybdenum, boron, vanadium and selenium). Sub-chapters deal with the question of CO_2 limitation and with vitamins and growth promoting substances as limiting factors. Besides the author details the microbial

strategies counteracting growth limitations (increase of surface-to-volume ratios, having intracellular storage capabilities, phosphatase activity, ability of N_2-fixation or transformation of sulphur compounds, utilizing organic compounds as energy and nutrient sources, to resist sinking, attachment to surfaces and symbiotic associations) and bioassay tests (bottle test, employing cultures of a single test alga, continuous flow chemostat test, also employing a single test alga and in situ test designed to measure the response of a natural primary producer community to nutrient enrichment) for determining factors limiting primary productivity in freshwater.

Chapter 4. F. B. van Es and L.-A. Meyer-Reil: Biomass and metabolic activity of heterotrophic marine bacteria. Heterotrophic bacteria play an important role in nutrient cycling of the sea and they are also members of the food web. The authors discuss the methods developed for determination of bacterial numbers and biomass, namely the direct-counting methods, especially epifluorescence microscopy, viable count techniques and chemical determination of special substances (ATP, bacterial cell-wall constituents). Though bacterial numbers and biomass yield valuable information on bacterial communities and their interdependence with other organisms, they do not necessarily reflect the dynamics of these communities. Methods for determination of bacterial activity as biological oxygen consumption rate, diurnal oxygen curve analysis, heterotrophic ^{14}C-fixation, uptake of labelled organic substances including the kinetic relations, rate of nucleotide incorporation into DNA and RNA, activity-changes of certain enzymes, frequency of dividing cells (FDC-method) and methods based on increase of bacterial cell-density in incubators (glass-bottles, dialyzing bags, etc.) are detailed. Considering that the methods discussed in the study are also widely used in freshwater ecology, the material is very useful not only for oceanologists but for freshwater bacteriologists as well.

Chapter 5. R. Y. Morita: Starvation-survival of heterotrophs in the marine environment. The author uses the term "starvation-survival" to indicate the processes (except for spore-forming) of survival in the absence of energy yielding substrates. Miniaturization of bacterial cells (as a newly recognized fact), endogenous metabolism, changes in cellular components, substrate-capture, chemotaxis and substrate uptake are mentioned.

Chapter 6. M. Fletcher and K. C. Marshall: Are solid surfaces of ecological significance to aquatic bacteria ? Over the past ten years bacterial attachment has received growing attention. Essentially all non-biological surfaces are eventually colonized by bacteria and only certain surface areas of plants and animals are apparently protected from colonization. Dozens of new methods were devised or adapted to focus on the problem. The authors mention the characteristics of the surfaces (physicochemical factors, which include chemical and thermodynamic features, physical factors, such as surface texture and biological factors significant when the substratum is another organism) and with conditioning films forming by a spontaneous adsorption of macromolecules at the solid-liquid interface. Other parts of the study analyse the mechanism of bacterial adhesion, the bacterial nutrition relative to the trophic status of waters, the ecological advantages of the attachment and succession and microbial film development. Although the review has been concerned with the significance of bacterial attachment in an aquatic environment, as the authors point out, essentially all environments inhabited by bacteria are "aquatic". Thus, it is likely that the problems progress and principles which apply to microbial attachment in natural waters will be relevant to other habitats (such as terrestrial environments where bacteria colonize soil particles and detritus) where attachment plays a significant role.

The current volume of Advances in Microbial Ecology is of great use to those involved in the fields of microbiology, limnology, algology, ecology, agronomy, marine biology and food science and technology.

J. Padisák

J. Calkins (ed.): The Role of Solar Ultraviolet Radiation in Marine Ecosystems. Plenum Press, New York–London 1982, xvi + 724 pp.

This monograph contains 58 papers, the whole material of a conference of the same title, held July 28–31, 1980, in Copenhagen. The authors and contributors are specialists from fields including atmospheric chemistry, biological radiation dosimetry, UV optical oceanography, aquatic photochemistry, and UV molecular photobiology.

It is the high time to realize that the human technology has become so effective that we can substantially modify and damage the gigantic and remote outer limit of our planet, the stratosphere. This fragile shell wich shields life on earth from the solar UV radiation of demonstrable injurious potential, may be destroyed by the human technological activities.

It is obvious that if stratospheric ozone layer were reduced and consequently the intensity of solar UV radiation reaching the earth's surface were increased, then human skin cancer would also be increased. But how does one even begin to estimate the impact of changed UV radiation on such a diverse, interacting and complex ecosystem as the oceans?

In this volume an international group of scientists provides both an outline of methodology and the specific details needed to evaluate the role of solar ultraviolet radiation in marine ecosystems.

To reach an organism of a marine ecosystem, the UV flux must penetrate first the athmosphere than — partly — the hydrosphere, too. This gives the natural structure of the volume: three sections.

In the first section (Atmosphere) 19 papers deal with the physical processes of atmosphere connected with solar UV radiation and their measurement. The main topics are: the measurement of the solar UV flux, photochemical reactions producing and destroying ozone, transmission of solar UV to the earth's surface, possible anthropogenic influences on strathospheric ozone. Another basic problem is the biological dosimetry of UV radiation. Several papers are centered around these questions: action spectra, dosage units and dosimetry of biological effects of UV radiation.

The second section (Hydrosphere) is centered around one basic question: how much solar UV reaches the living organisms at various depths in natural waters? The attenuation processes, scattering and absorption, combine in complex ways to produce the effective attenuation. Several papers are devoted to the problem of calculating the diffuse absorption coefficient and the overall attenuation coefficient in marine waters. Just as the ozone shield in the atmosphere, there is a component of the natural waters, the "yellow substance", which is the most effective in absorbing solar UV. But it is unique to the oceans that the living organisms may undergo the complete possible range of exposure as they move about in the water column either actively controlling their position or passively carried about by the water movement.

More than the half of the volume is devoted to the biological aspect of the topic (Biosphere). 33 papers deal with the effects and responses induced by solar UV in the aquatic biota. The main topics are: the primary photochemical lesions and defending tactics induced by UV radiation, mechanisms of repair processes after UV induced damage, sensitivity to UV radiation in different types of marine Biota, effects of UV flux on photosynthesis of phytoplankton, evolutionary effects of solar UV, adaptation strategies and photomovement of aquatic organisms.

Among the specific studies, directed to the biological response of a certain species of group of species, one may find reports on fish larvae, adult fish, algae, crustaceans and other economically important marine species in connection with their responses to solar UV.

The whole volume is well-prepared and documented with many figures and diagrams, microphotos and tables. It is supplied with a subject index.

Highlighting an important ecological problem, this book will be of interest to ecologists, photobiologists, microbiologists, hydrologists and even meteorologists.

Z. Szőcs

F. I. Woodward–J. E. Sheehy: Principles and Measurements in Environmental Biology. Butterworths, London 1983.

This long-needed book has been written for everybody who wants to get a deeper insight into the important physical principles of environmental biology and their application to actual studies. A conceptual framework including both theoretical and practical aspects of measuring physical parameters of environment is presented. The authors are successful in providing a well-balanced treatment of physical, biological and intrumental problems of environmental biology. Their wide knowledge of the subject is a guarantee that this book is worth reading before any measurements are taken in the field.

The book consists of eleven chapters, an Appendix and an Index. No separate bibliography is provided, dozens of references are listed at the end of each chapter. It seems a good idea that symbols used in the text are summarized at the beginning of each chapter.

Chapter 1 is a review of the environmental effects on plants and animals. Solar radiation, temperature, water, atmospheric pressure, air flow and carbon-dioxide concentration are selected for discussion. The physical principles related to these environmental factors are presented in Chapters 2 to 4: one is informed about the wave and quantum theories of radiation, measurement of photosynthesis, gas laws, effusion and diffusion, water flow, osmosis, tensions, laws of thermodynamics, etc. This part of the book, as the above list demonstrates,

gives a strong background of physics for the reader. The numerous examples supplied are most useful for environmentalists.

Chapter 5 deals with the micrometeorology of vegetation. Emphasis is on air movement and temperature. Chapter 6 summarizes some basic principles of sampling environmental parameters. Clear distinction is made between spatial and temporal sampling. Some useful hints are given and several practical problems of sampling are exemplified, but very little is said about sampling theory and its relevance to environmental studies. Therefore, readers interested in sampling problems should also consult with other books. This statement also applies to the next chapter, which is a brief account of measurement errors through a discussion of elementary statistical concepts.

Chapters 6 and 7 describe transducers, display and recording devices. The mechanism of operation of these instruments is discussed in detail. References to older techniques are also given.

Chapter 10 includes three case studies to illustrate practical applications of the methods discussed previously. Two cases are concerned with aerodynamic techniques applied in different ways. The third case study describes the design of an enclosure apparatus for crop studies. Chapter 11 provides an introduction to some important growth analytical concepts and also includes a case study.

In summary, this book is a very useful reference guide and may be recommended to all students of environmental biology.

J. PODANI

V. SCHULZ–F. W. WHICKER: Radioecological Techniques. Plenum Press, New York 1982, 298 pp.

In the introduction to this book the authors claim that this is not a working manual for radioecological techniques developed for use in ecology; rather it was the wide assortment of radioecological techniques that may lead to unique scientific advances. For this reason they were faced with the enormous task of selecting from a very large number of papers available, those that would reflect the diversity in ecological techniques that involve radionuclides and ionizing radiation as well as those that illustrate the ingenuity of ecologists and contributions to the understanding of ecosystems.

The volume consists of eleven chapters, an Appendix with the physical characteristics of radionuclides discussed in the volume, a list of Literature Cited (418 items), a list of Additional Readings (232 items), and finally an Index.

Chapter 1. Introduction. Besides general comments there is a short summary of those proceedings, books, manuals and reviews concerned with the various radioecological studies.

Chapter 2. Dating Techniques. This chapter deals with the technique of radiodating geological and biological specimens which has been accepted as a powerful tool by archaeologists, geologists, and biologists. Authors describe the concepts briefly and then mention the substantial methods, such as carbon-14, potassium-argon, uranium series, thermoluminescent and fission-track dating.

Chapter 3. Neutron Activation. This method has been readily accepted by environmental biologists due to its advantages. It might be useful in studies of ecosystems in populated areas where use of radiotracer would not be desirable. We can find examples for use of activation analysis both in terrestrial and aquatic systems.

Chapter 4. Autoradiography. This widespread method may be used in terrestrial studies; for distribution of the tracer after a period of time, for recognition of a food-chain, for investigating pesticides, herbicides within an organism as well as within the ecosystem, etc. Autoradiography is also utilized in marine and freshwater biological studies to investigate the fallout radionuclides in natural systems, the uptake and distribution of tracers, the primary productivity in aquatic ecosystems, and pesticide biodegradability, etc.

Chapter 5. Radiation Sources and Dosimeters. The authors have briefly summarized the essence of radiation methods: „Radiation must be considered as a form of stress that can be applied with safety and precision to natural ecosystems. Community responses to radiation stress reveal many basic aspects of ecosystem structure and function, and for this reason, radiation may be considered as a technique to develop fundamental ecological knowledge."

After this they discuss the most important radiation sources developed for field studies. The third part of this chapter deals with the dosimeters which estimate quantity of ionizing radiation. Different types (e.g. solid-state, thermoluminescent, glass-rod dosimeters, ionization chambers and film badges) are also demonstrated.

Chapter 6. Behavioral Studies. This more detailed chapter deals with the importance of field studies in population dynamics. The radionuclide tracer technology provides an opportunity for investigations related to population dynamics. Tag-recapture procedures are good for population estimation, determination of home range and other behavioral studies. Further on General Comments give particulars of radiotracer methods of tagging, their advantages compared with the limitation of the standard methods, and their disadvantages.

The subdivision "Invertebrates" states that applications of radionuclides in behavioral studies of insects are numerous while applications of studies of other invertebrates are very limited. Isopod, yellow ant, leaf bug, blackflies, ticks serve as examples. The subdivision "Vertebrates" deals with fishes, amphibiants and reptiles, birds, and mammals. In the case of amphibiants first of all the movement and hibernation stage were studied both above and below ground. It is possible to become acquainted with the various types of radioactive tagging procedures developed for small mammals, bats, water vole, rats and larger mammals, as rabbit, fox, etc.

Chapter 7. Hydrological Studies. In this chapter the sediment movement studies are demonstrated chiefly with some tables as "List of Techniques and Quantities of Radioisotopes Used", "Methods for Labeling Sediments with Radionuclides" and "Investigations Using Radionuclide Markers to Study Sediment Transport". Radionuclides are also used to study oil pollution, dispersal of sewage in the sea, pattern and extent of eddy diffusion, and river flow times. Soil-moisture determination is available by the aid of neutron moderation or by means of gamma-ray transmission.

Chapter 8. Physiological Studies. Identifying a labelled compound is the topic of this chapter. Among terrestrial organism, in plants many compounds have been labelled with ^{14}C, since all organic compounds contain carbon. For example effects of temperature on the respiration of sugars in willow was studied by this method. Another radionuclide commonly used in physiological studies is the isotope of hydrogen known as tritium. Beside it iodine-131 is a widely used radionuclide in animal physiology to measure metabolism. In water plant physiology the use of radionuclide tracer method is unknown to the authors.

In the case of aquatic animals several scientists use radionuclid labels, e.g.; ^{14}C in the case of the glucose uptake by coral. ^{45}Ca on calcium accumulation by sea urchin eggs, ^{32}P at the uptake and release of inorganic phosphorus by the plankton crustacean *Daphnia magna*.

Chapter 9. Primary-Productivity Determination. Primary productivity and its measurement in an aquatic system by ^{14}C method is well known since it was proposed by STEEMANN NIELSEN. The authors comment on the various steps of the procedure to clarify some aspects of this technique because that is relatively simple, but the interpretation of the results is not.

Chapter 10. Cycling Studies. This is the longest chapter justified by its importance and scope. This field contains the uptake, retention, and excretion of stable elements by organisms as well as the total pattern of mineral cycling within and among ecosystems.

"Ingestion" is begun by mentioning the classic method of SOROKIN (1968) and continued by the new technique of CALOW and FLETCHER (1972). After this the authors cite countless examples and literature for feeding rates of terrestrial invertebrates, for insect-plant relationships, for ingestion rates of microarthropods, for feeding rates and food utilization of caddisfly larvae, for filtering rates of molluscs, for feeding rates of fishes, not to mention the others. Biological uptake and retention is the second most important question. Studies are concerned with the nutritional aspects of essential to age and antler growth, mineral metabolism of various types of aquatic organisms, marine zooplankton element-elimination rate, biological uptake and retention of fission and neutron-activation products in organisms including man and domestic plants and animals.

The part under "Excretion" deals with the use of tracers in studying food-passage rate in animals. The questions of the ecosystem are discussed in the second part of this chapter from the food web to the "complete" system or subsystem both in terrestrial and aquatic points of view.

Chapter 11. Miscellaneous Techniques and Equipment. Under three headings ("Environmental Pollutants", "Sterile-Male Method of Insect Control", and "Other Techniques") the authors give a summary of those techniques that seem to be of marginal relevance to the other sections of this volume.

This volume is a well-documented, comprehensive work and the authors may be commended in their tremendous efforts to give an up-to-date synthesis of radioecological techniques. This book summarizing the results and aspects of different biological disciplines is very useful for all scientists dealing with ecology.

N. OERTEL

G. LERCH: Pflanzenökologie. Teil I und II. Akademie-Verlag, Berlin 1980, 205, 216 pp.

The book, published as the 262nd and 263rd volumes of the popular series "Wissenschaftliche Taschenbücher" (WTB) of the Academy Publishing House, Berlin is the third revised and enlarged version of the Author's work, issued earlier in already 2 editions. The book consists of two volumes separating from each other also in their topics.

Volume 1

The first volume entitled "Life of the Plants in their Natural Environment" (Das Pflanzenleben in seiner natürlichen Umwelt) deals with the analysis of the individual ecological factors and the effects thereof exercised on the plants and plant communities and with their mutual connections, respectively.

When describing the ecological factor, the temperature to be presented first, a detailed analysis is given of the heat budget of the soil and plants, the radiation conditions in connection with the temperature, the warm effect, the heat-resistance and the cold effect as well as the temperature conditions of the alpine vegetation.

The second large topic is water ecology. After the atmospheric water, the precipitation conditions of the Earth, the direct and indirect influence of the dew and fog had been described, the subsoil water oecological factors are presented. This is followed by the description of the oecology of the water intake and loss. The chapter parts on the water balance, xerofitons and their water budget respectively, are thoroughly worked out.

In the chapter of light ecology mainly the connections between the sun plants and shade-living ones and leaves, respectively, are studied under the interconnections between the light ecology of germination and the particular forms of growth (lians, epi- and hemiephyfitons) determined by the light as well as between the day length and the dispersal of the plants.

The chapter including chemical factors gives an analysis first of the carbon dioxide, oxygen and mineral matter conditions of water as medium of life. In the detailed chapter of soil ecology the following important points are included: decay, building up of clay, disintegration, soil types, humus, ecology of mineral matter intake, soil conditions and the dispersal of the plants, the soil profile and soil types. Then a picture is given of the ecology of the special habitats: salty areas, mangroves, dunes, bogs (fens and high bogs, heides) rocks and talus slopes. Volume 1 ends with the description of the mechanical factors (wind, snow, burning, mowing, grazing and animal mastication).

Volume 2

The volume entitled "To the Ecology of Material Production and Fruit Formation" (Zur Ökologie von Stoffproduktionen und Ertragsbuilding) includes the effect of the outer and inner factors having an influence on the plant production, the productivity of plant stands, the production ecology of selected plant communities and the biochemical cycle. In the chapter entitled "The effect of the outer factors" a comprehensive survey is given by the author of the influence of the light, temperature, carbon dioxide, water and mineral matter supply on the CO_2 assimilation. In this chapter the effect of the different damaging materials (sulphur dioxide, fluorine, and hydrogen chloride, photochemical contaminating materials, dust deposits, plant protectives), and that of the waters are described.

The chapter entitled "The effect of the inner factors" makes one acquainted with the changes of the production depending on the age, state of development and forms of growth of the plants.

In the chapter dealing with the productivity of the plant stands the leaf area index (LAI), growth indexes (NAR, RGR) and the questions of the production balance are discussed.

The following chapter, dealing with the production ecology of certain vegetation types is written with a rather successful comparative approach of production ecology. The given vegetation types are: polar tundra, boreal pine-wood, deciduous wood, evergreen tropic rain-forest, grassland and water associations. Within the scope of object of the biochemical cycle the cycles of the carbon, nitrogene and water within the ecosystems and in the Earth, as well as the effect and consequences of the human intervention are shown by the Author.

The book ends with chapter dealing with the plant production and problem of supplying the world with food, according to which one of the keys solving this problem may be a product increase based on the modern ecological view.

With this work written by Gerhard LERCH, a book is given in the readers' hands, wherein all the important fields of ecology are described, reflecting the already accepted, settled results. To support and demonstrate what he wanted to say, the author successfully chose the literature of a great number and real importance. The tables (32) and charts (116)

are expressive and essential. The editorial work as well as the typographical get-up of the book deserve praise.

Gerhard LERCH's ecological book can be recommended with full reason to the attention of not only the ecologists and students but also of those working in other fields of biology.

Z. TUBA

R. HUNT: Plant Growth Curves. The Functional Approach to Plant Growth Analysis. Edward ARNOLD Publishers Ltd., London 1982, 248 pp.

In addition to thousands of articles and several books devoted to plant growth analysis, a new book has come out recently which gives an insight into the functional approach to plant growth analysis. The author's name, R. HUNT is well known among those dealing with this topic. In his newest book he provides a thorough review of functions recently used more extensively in describing the course of plant growth.

The book consists of eight chapters and is completed with an abundant reference list, a subject and an author's index.

The first chapter is an extended overture. A chronological review of growth analysis, its relations to other fields (e.g., community production, population demography, photosynthetic production, etc.) and the differences between the classical and functional approaches are discussed. The author enumerates the units (SI) used in the text, as well as the notations.

The second chapter reviews the measured and derived quantities or characteristics used in plant growth analysis at the individual (RGR, LAR, ULR, etc.) and the supra-individual (i.e., population or community) level (LAI, CGR, LAD, etc.). A comprehensive table including these quantities is also presented.

In accordance with the sub-title, the subsequent chapters deal with different approaches and describes functions used in plant growth analysis. The third chapter could be considered as a fundamental and/or starting one. It makes us acquainted with the theoretical principles (mechanistic and empirical models) and also refers to the advantages of curve fitting. It is demonstrated how the quantities described in the second chapter can be derived from curves fitted to the transformed and non-transformed observational data.

The fourth chapter is devoted to the application of function fitting. The author distinguishes among many kinds of fittings depending on the primary data (derived from indirect or direct estimations) and whether the aim is to insert the values derived from primary data in the classical formulae or to establish the instantaneous values. The subjective free hand curve fitting (by eye) is distinguished from the objective statistical methods.

The following chapters review the application and utility of the various function families. The polynomial functions are discussed in the fifth chapter. After a brief theoretical introduction, the first-, second-, third-, and higher-order polynomials and their properties are treated separately. Every section is completed with case studies exemplifying applications of various functions. These are summarized in tables in which the relevant literature plant species, primary and derived data are also indicated. The stepwise polynomials section reviews the successive addition of polynomial terms.

In the sixth chapter are discussed four widely used (monomolecular, logistic, GOMPERTZ, RICHARDS functions) and other less known functions, termed the asymptotic functions. This chapter is similar to the previous one regarding structure. After the theoretical part, the applications of functions are presented. Other asymptotic functions are derived from one of the functions mentioned above by modifications on empirical bases.

In the seventh chapter the applications of the various combinations of individual functions are discussed. An idea like this can be found in the segmented regression analysis. Plant growth can also be described in terms of other approaches, e.g., segmented and splined regression and the method of running re-fits.

The last chapter is the analytical summary of the others. The rationale of plant growth analysis and the future possibilities of its application are outlined using many references.

The book is an excellent summary on the field of plant growth analysis. The extensive bibliography provides information indispensable for anyone dealing with this topic.

E. MOLNÁR

A. D. GORDON: Classification. Methods for the Exploratory Analysis of Multivariate Data CHAPMAN and HALL, London. 193 pp.

Classification has long been a major objective in botanical research. Taxonomists and ecologists have contributed much to the development and popularization of numerical classificatory techniques. A literature review would certainly support my contention that cluster analysis may well have the highest number of applications in botany. Conversely, most of the users of cluster analysis are not familiar even with the elements of numerical classification. This book, although written for a wider audience including statisticians, may be helpful in this regard. Belonging to the "Monographs on Applied Probability and Statistics" series, it is an excellent introduction to cluster analysis and related techniques.

The contents of the book appear well-balanced. In Chapter 1 the subject is introduced by reference to several examples including two botanical problems. The purposes and desiderata of a classification are summarized and the main types are described. Chapter 2 discusses types of variable and presents several measures of dissimilarity. This section is by no means complete, only the most commonly used formulae are mentioned. The problems of weighting, mixed variables and missing values, potentially encountered when selecting a dissimilarity measure, are also outlined.

Chapter 3 describes a general algorithm for agglomerative clustering with emphasis on the single link and sum of squares methods. Of the non-hierarchical techniques the iterative relocation algorithm is discussed. Some remarks on the links between clustering and more formal statistics are also given. The author stresses the importance of further research towards the synthesis of cluster analysis and statistical methodology.

Chapter 4 is in fact the continuation of the preceding by describing selected, more sophisticated procedures such as clumping, fuzzy clustering and constrained classification. For an average reader this section provides much more new information than Chapter 3, but one may still have the feeling that a fuller discussion of clustering methodology could have been included. For example, although the often-criticized monothetic divisive technique of LANCE and WILLIAMS is discussed, the agglomerative techniques based on similar information theory considerations are ignored.

An obvious advantage of the book is that its topic is not restricted to cluster analysis sensu stricto. Instead, geometrical techniques such as multidimensional scaling represent a vital part of the monograph. As the author repeatedly emphasizes, exclusive use of clustering methods may result in misleading conclusions if a classification is imposed on data without any real group structure. Accordingly, joint application of scaling and clustering methods is recommended. Selected techniques of scaling, e.g., principal coordinates analysis, non-metric multidimensional scaling and correspondence analysis are described in detail in Chapter 5. This is perhaps the most difficult section for non-statisticians, some parts are impossible to follow without a thorough knowledge of matrix algebra.

Chapter 6 is a brief discussion of various approaches to the assessment of classifications including hypothesis-testing and the comparison of results. Many useful hints are provided but the methodological basis presented seems insufficient. Results of some case studies are discussed in Chapter 7. Two cases may be of interest for the readers of Acta Botanica, namely the classification of pollen spectra and soil profiles. Different techniques are applied to each problem illustrating the superiority of the simultaneous use of scaling and clustering over the straight cluster analytical approach.

As a whole, the book is a valuable contribution to the literature of cluster analysis. It should not be absent from libraries and is recommended for individuals interested in classification theory. This book is very useful for beginners seeking methods suitable to the analysis of multivariate data.

J. PODANI

D. C. WEST–H. H. SHUGART–D. B. BOTKIN (eds): Forest Succession. Concepts and Application. SPRINGER Verlag, New York–Heidelberg–Berlin 1981, 517 pp.

This book is a summary of the results presented at a conference held in Mountain Lake, Virginia, 1980. Most contributors are from the American continent.

The papers differing widely in basic situations, approaches and concepts are grouped into four sections.

The chapters of the first section discuss basic concepts, specific theoretical aspects and applications. An introductory paper is written by O. LOUCKS. An essay by R. P. MCINTOSH examines the historical development of relevant literature and the contribution of succession

studies to ecological theory. The subsequent papers give a quantitative analysis of successional variables in simulation models. Three principles are applied: 1. Collective, emergent features of the communities can be based on the demography of species; 2. Occasionally, functional groups can be formed instead of species; and 3. It is a constant task to develop and test hypotheses. In some models treated the external perturbations are taken into consideration. Their role in gap-dynamics is discussed by Th. DOYLE. One of the best written papers in this section is: Patterns and dynamics of forest: An application of simulation models (by H. H. SHUGART, D. C. WEST and W. R. EMANUEL). Four relative models are described which consider the following common processes: growth of trees under optimal conditions; height/diameter; leaf area/light-extinction, reduction of photosynthesis due to shading; crowding effect, tree mortality. Composition dynamics in the different forest communities is then studied by using these models, simulating the natural state and perturbation (e.g., forest fires).

Another group of papers demonstrates methods dealing with the relative long time scale of forest succession. These explorations consider available records of prehistoric forest dynamics. The paper by J. WALKER, C. H. THOMPSON, J. F. FERGUS and B. R. TUNSTALL (Plant succession and soil development in coastal sand dunes of subtropical Eastern Australia) shows a complete change in plant life forms through time: herbs are replaced by shrubs and then by trees during succession. Pollen evidences are utilized in two chapters.

From Chapters 13–16 the lesson can be drawn that communities, even though dominated by species of the same life form, can differ considerably in successional features. However, all forests studied here are evergreen, and the scales of temporal and spatial dynamism are very different. Potential reasons for these differences are: the life history of the constituting species, the size of plant individuals, morphology, species diversity, climate, soil, and seasonality. In the boreal forests of Alaska a well marked direct connection is observed between the quality of vegetation and the physical environment, so succession is a constant process and its states can be predicted. It appears that vegetation is very important in determining the nature of change (K. Van CLEVE, L. A. VIERECK: Forest succession in relation to nutrient cycling in the boreal forest of Alaska). On the contrary, succession in the tropics, as described by A. GOMEZ-POMPA and C. VÁZOUEZ-YANES, is an even more complex process. There are so many species capable of filling a particular niche that emphasis was placed on physiognomy and tree physiology (growth rates, seed size, dormancy and tree geometry). Ranking among different species is a rather than on taxonomy. Vegetation-changesare determined by the characteristics of life history of the succeeding species.

After all, chapters of this section fail to support a monolithic unifying theory of forest succession. Therefore, methods of studying succession must be adjusted to fit the particular characteristics of the region.

In the last section several papers analyze the background processes (for example, nutrient cycling: P. M. VITOUSEK, P. S. WHITE; changes of biomass and production: R. K. PEET; above-ground biomass accumulation: A. W. COOPER; below-ground processes: K. CROMACK) but further case studies are also included in this section. The outstanding article by K. D. WOODS and R. H. WHITTAKER sets itself an aim to enlighten the inner mechanisms (Canopy-understory interaction and the internal dynamics of mature hardwood and hemlock-hardwood forests). On the basis of their methods, they succeeded in pointing out the different organizing effects of the species of tree layer on the understory. Data of such nature can be used in forming schemes of species substitution as well. One of the main conclusions of the paper is that the understanding of requirements and limitations of important species in early stages of their life cycles is generally necessary for adequate explanation and understanding of community dynamics.

The attractive book is well illustrated throughout. One of its main merits is that the different views formed in connection with forest succession are presented such that attention is paid both to the theoretical and the empirical appreaches. No question that this book is indispensable for those dealing with the theoretical and practical aspects of succession.

G. FEKETE

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INTERCELLULAR SYMBIOSIS OF NITROGEN-FIXING BACTERIA AND GREEN ALGA

I. GYURJÁN, I. TURTÓCZKY, G. TÓTH, GY. PALESS and N. H. NGHIA

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(Received: 17 January 1984)

The unicellular green alga, *Chlamydomonas reinhardii* was forced into association with different species of nitrogen-fixing *Azotobacter* in nitrogen and carbohydrate-free medium. On the basis of growth and nitrogenase activity *A. vinelandii* is the most effective species examined by us and presumably the most perspective partner in associative symbiosis.

Scanning electron micrographs reveal that bacterial cells are localized close to the surface of algal cells. There are nearly 2–3 times more bacterial than algal cells in associative cultures. The chlorophyll content and similarly the rate of photosynthetic O_2 evolution of them is nearly the same as the value obtained with the control. These data suggest that associative cultures are photosynthetically active and able to meet energy required for nitrogen fixation.

Introduction

Nitrogen is an essential element for life and with the exception of water, it is the most common limiting nutrient in agricultural practice. The main part of the nitrogen plants need comes from the atmosphere, mainly with biological nitrogen fixation.

The biological nitrogen fixation is carried out by prokaryotic organisms (bacteria and blue-green algae) and the most effective systems are different types of symbiotic associations with plants (YATES 1976).

The term "associative symbiosis" was used by BURNS and HARDY (1975) to denote those N_2-fixing associations between prokaryotes and eukaryotes in which the prokaryote when isolated and grown free from the host, could fix N_2. It was always difficult to distinguish between free-living and associative N_2-fixing prokaryotes. Rhizobial-legume associations may also be regarded as associative symbioses.

In recent years the associations of N_2-fixing prokaryotes with various crop plants, distinct from legumes, have a potential importance and they are currently one of the most interesting and speculative areas of N_2-fixation research (STEWART et al. 1979).

In the non-nodule forming associations the N_2-fixing prokaryotes occur in association with leaves and roots of higher plants (RUINEN 1975, KNOWLES 1977). A large number of higher plants take part in these types of symbioses as well as a lot of N_2-fixing bacteria e.g. the following species: *Azomonas*, *Azospirillum*, *Azotobacter*, *Beijerinckia*, *Clostridium* etc. Physiological and biochemical analyses of such types of symbioses help us to make new, artificial symbioses from loose associations to very close symbioses, involving endosymbioses as well. The factors affecting the successful establishment of such N_2-fixing systems are complex, but depend on at least five major factors: the specificity of associations, a fairly steady ratio between the biomass of the eukaryote in the symbiosis, and morphological, physiological and biochemical modifications of the partners.

In this paper a morphological and physiological analyses of an artificial association between aerobic bacteria, *Azotobacter* and unicellular green alga *Chlamydomonas reinhardii*, is presented.

Material and methods

Strains and growth

Four species of strictly aerobic, nitrogen-fixing *Azotobacter*, *A. chroococcum*, *A. beijerinckii*, *A. agilis*, *A. vinelandii* were used (Fig. 1). The cells were grown in nitrogen-free medium, in liquid culture (NEWTON et al. 1953).

To construct growth curves, cultures had been incubated in Erlenmeyer flasks in a shaker at 28 °C for 30 h. Samples were taken every two hours for measuring the number of the living cells and optical density.

The unicellular green alga, *Chlamydomonas reinhardii* (Fig. 2) was forced into association with *Azotobacter* cells described above. A combined nitrogen and carbohydrate free medium was used for bacteria-alga associated cultures. The medium consisted of (per litre): K_2HPO_4, 1 g; KH_2PO_4, 0.4 g; $CaCl_2 \cdot 2\ H_2O$, 0.05 g; $MgSO_4 \cdot 7\ H_2O$, 0.2 g; NaCl, 0.3 g; $CaCO_3$, 0.25 g; $ZnSO_4 \cdot 7\ H_2O$, 0.02 g; H_3BO_3, 0.02 g; $Na_2MoO_4 \cdot 2\ H_2O$, 0.008 g; $MnCl_2 \cdot 4\ H_2O$, 0.005 g; $FeSO_4 \cdot 7\ H_2O$, 0.005 g; KI, 0.0005 g; NaBr, 0.0005 g; $Al_2(SO_4)_3$, 0.0003 g; $CoCl_2 \cdot 6\ H_2O$, 0.002 g; $CuSO_4 \cdot 5\ H_2O$, 0.002 g.

Measuring the chlorophylls

Chlorophyll content of algal-cells was extracted in 80% (v/v) acetone and estimated from the absorbance data measured at 642 and 661 nm by the formula of AVRON (1960).

Measurement of photosynthetic oxygen evolution

An oxygen sensitive RA-9503 type combined Ag/Pt electrode was used for measuring O_2 evolution in light. Cell density was approximately 10^6 cells $\cdot$ cm^{-3} while temperature and illumination were 25 °C and 20 000 lux respectively.

Electron microscopy

Harvested cells had been fixed in 1% glutaraldehyde (2 mM K-Na phosphate buffer, pH 7.2) for 2 h. After thorough washing, there is a post-fixation in 1% OsO_4 using the same buffer for 2 h. The samples were dehydrated in ethanol series and propylene oxide, then embedded in Durcupan ACM (Fluka). These sections were made with a Porter-Blum MT-1 ultramicrotome, stained with uranyl acetate and lead citrate and then examined with Tesla BS-500 electron microscope.

Scanning electron microscopy

The cells were spread over a small aluminium foil in thin layer and fixed in 2.5% glutaraldehyde (at room temperature for 1 h) washed in 0.1 M cacodylate buffer (pH 7.4). Then the specimens were washed three times in the buffer at room temperature, dehydrated in ethanol series and amylacetate, and dried using CO_2 in a Du Pont critical point dryer (CT 06470). All specimens were mounted on stubs with a Dotite silver adhesive and coated with gold. Examination were made with a Jeol 50/A scanning electron microscope at 15 kV.

Acetylene reduction assay

Samples (8 ml) of the culture were placed in 25 ml serum vials. The vials were fitted with rubber stoppers, and 5 ml air was withdrawn from each. The C_2H_2 reduction assay was initiated by injecting 5 ml of C_2H_2 into each vial. Having a 10 hour incubation at room tem-

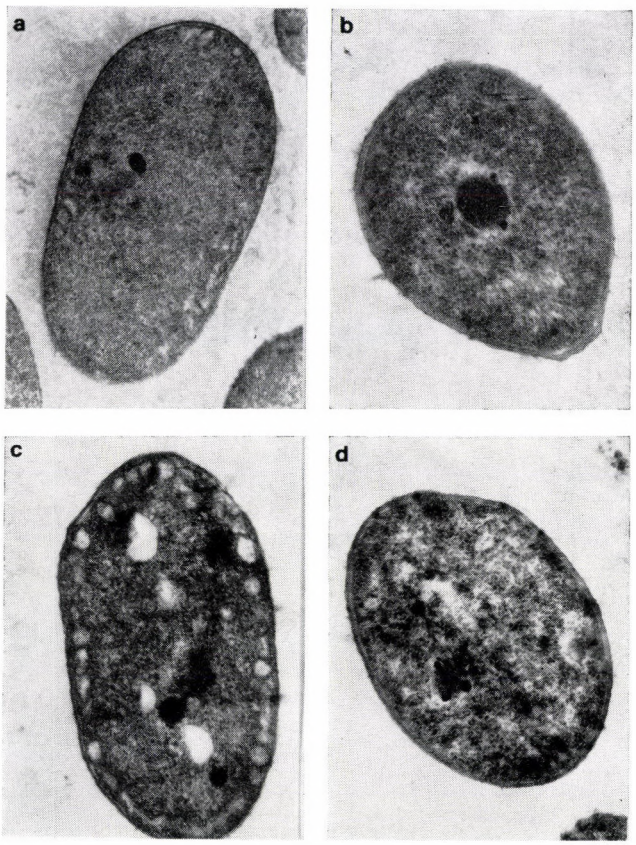

Fig. 1. Electron micrographs of *Azotobacter* cells. a) *A. chroococcum* (magn. ×27 000), b) *A. beijerinckii* (magn. ×65 000), c) *A. agilis* (magn. ×35 500), d) *A. vinelandii* (magn. ×50 500)

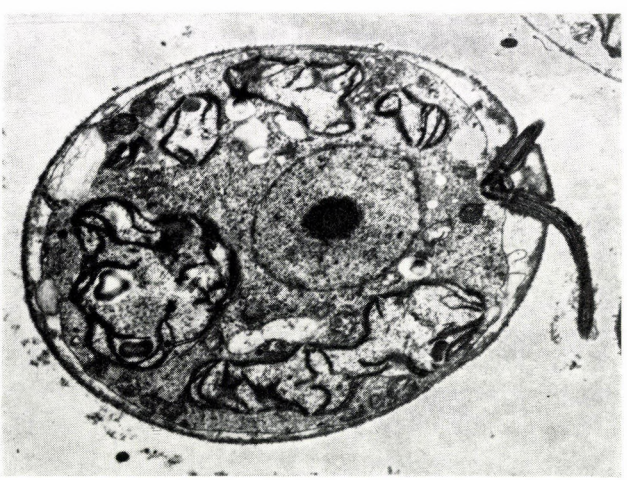

Fig. 2. Electron micrograph of *Chlamydomonas reinhardii* (magn. ×9000)

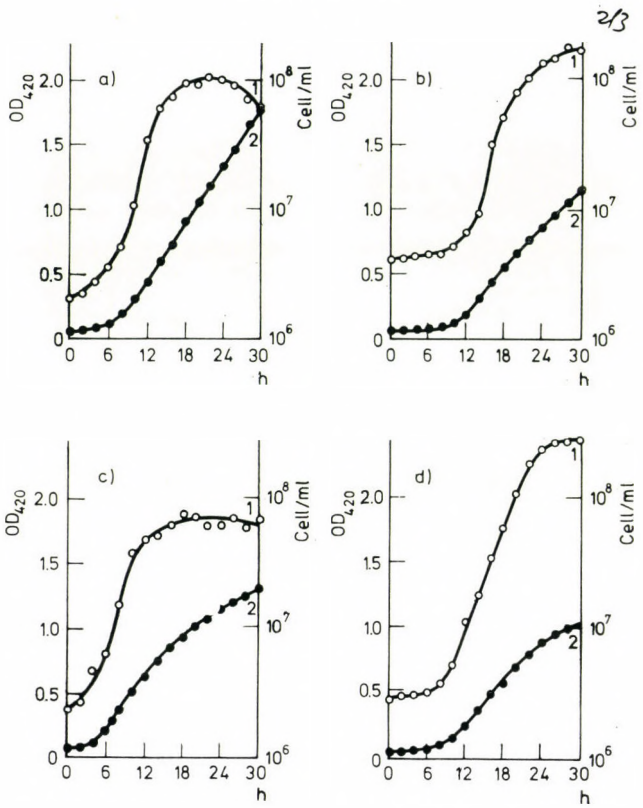

Fig. 3. Growth curves of the four *Azotobacter* species. a) *A. chroococcum*, b) *A. beijerinckii* c) *A. agilis*, d) *A. vinelandii*. 1 = cell number; 2 = O.D.

perature the gas samples (0.2 cm^3) were assayed for C_2H_4 using a Jeol model 1100 FP gas chromatograph equipped with a flame ionization detector and a column of Porapak N (150 × 0.3 cm).

Results and discussion

Growth of Azotobacter cultures

Growth curves, obtained from nearly the same amount of inoculum, are shown in Fig. 3.

Quantitative and qualitative differences are existing between growth curves of different species. The most important data arising from the curves are summarized in Table 1.

Worth noticing that parameters which characterize the growth of species are rather similar to each other, the only exception is *A. vinelandii*. Considerable increase in cell number during growth cycle, relatively long generation time characterize the latter.

Table 1

Characteristic data of bacterial growth curves

Species	Total growth $\left(\frac{\text{maximal cell number}}{\text{initial cell number}}\right)$	Specific growth rate μ_{max} (h^{-1})	Interval of exponential growth (h)	Generation time (h)
Azotobacter chroococcum	49.5	0.56	9–13	1.24
A. beijerinckii	41.7	0.48	12–18	1.44
A. agilis	30.0	0.45	6–10	1.54
A. vinelandii	102.0	0.30	10–22	2.31

Nitrogen fixation of Azotobacter cells

Ethylene production of the samples incubated for 10 h in an atmosphere containing acetylene is presented in Table 2.

A direct correlation exists between the characteristics of growth and acetylene reduction. Consequently, *A. vinelandii* is the most effective species examined by us and presumably the most perspective partner in associative symbiosis.

Scanning electron microscopic morphology of bacterium-alga associations

Associative cultures were produced by mixing *Azotobacter* and *Chlamydomonas* cells on agar plates, lacking all kinds of nitrogen and utilizable carbon sources (minimal medium). The cultures are showing slow but visible growth. The algal cells retained their green colour while control culture of *Chlamydomonas* on the same minimal medium turned yellow and died within 2 months. Some of the associative cultures have been living for more than a year by now.

Structural characteristics of settled cultures (having lived for half a year on minimal medium) were investigated by scanning electron microscopy.

Table 2

Nitrogenase activity in Azotobacter cells

Species	nmol of ethylene / 10^8 cells · h
Azotobacter chroococcum	1.12
A. beijerinckii	0,95
A. agilis	0.83
A. vinelandii	1.39

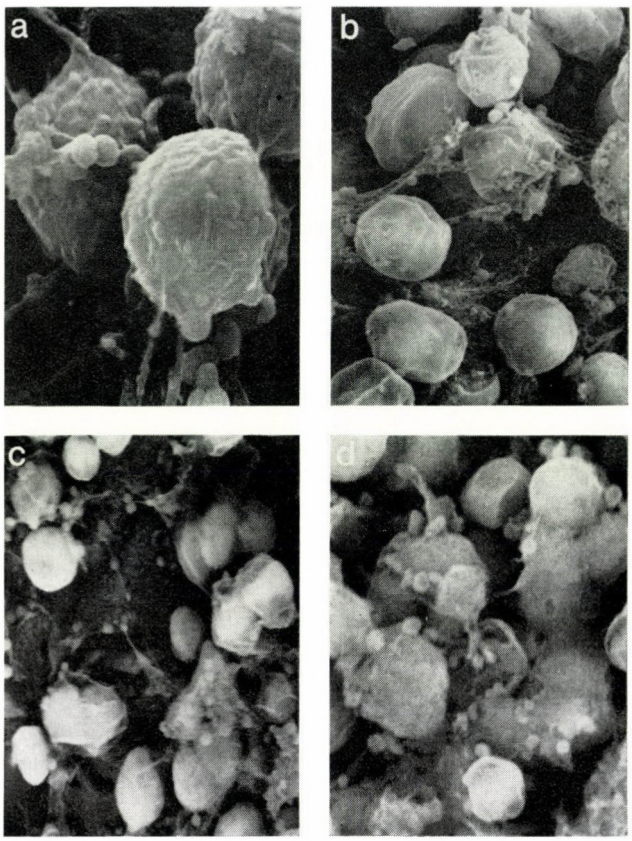

Fig. 4. Scanning electron micrographs of alga-bacterium associative cultures: *Chlamydomonas reinhardii* + a) *Azotobacter chroococcum* (magn. ×11 500); b) *A. beijerinckii* (magn. ×6000); c) *A. agilis* (magn. ×3500); d) *A. vinelandii* (magn. ×5000)

Electron micrographs (Fig. 4) show a few bacteria connected with each algal cells. They are localized close to the surface of the algal cells. The ratio calculated from viable counts gave 2–3 times more bacterial than algal cells approximately. In such a symbiotic system there seems to be an important factor the steady ratio between the biomass of the partners.

Photosynthesis of associated cultures

The photosynthetic effectiveness of algal cells in associated cultures were compared with control alga growing on a medium supplied with NH_4Cl (Table 3).

It is clear from the data, that the chlorophyll content of the cells is similar to that of the control having appropriate nitrogen supply. Similarly,

Table 3

Chlorophyll content and photosynthetic O_2 evolution of algal cells in associative cultures

Culture	Chlorophyll $a + b$ nmol per 10^7 cells	O_2 evolution per	
		10^7 cells	chl $a + b$
		%	
Chlamydomonas reinhardii (control)	28.8	100.0	100.0
C. reinhardii + *A. chroococcum*	23.8	91.1	110.6
C. reinhardii + *A. beijerinckii*	19.8	84.2	122.5
C. reinhardii + *A. agilis*	21.0	84.8	116.3
C. reinhardii + *A. vinelandii*	20.7	89.1	124.8

the rate of the photosynthetic O_2-evolution is nearly the same as the value obtained with the control. These data suggest that they are photosynthetically active. Considering the slow growth, it seems possible that carbon compounds are released by algal cells. So far glycolate excretion has been proved for *Chlamydomonas* (TOLBERT 1979) but still we have no data whether *Azotobacters* can utilize glycolate as a carbon source. On the other hand, such excreted materials can be taken up by bacterial cells from the medium.

On the basis of some naturally occurring associations between higher plants and free-living N_2-fixing bacteria (DÖBEREINER et al. 1972, BURNS and HARDY 1975, STEWART et al. 1979) it seems feasible to force these bacteria into symbioses with plant tissues. Hitherto nearly all of these forced associations aimed at the nitrogen supply of the eukaryote partner only and the energy requirements of nitrogen-fixation were met by carbohydrates added to the medium (CARLSON and CHALEFF 1974, BUTENKO et al. 1982). The question arises, whether autotrophic growth can be maintained in a symbiotic system, containing a so-called non-symbiotic nitrogen-fixing bacteria and a non leguminous photosynthetizing organism. On the basis of our data we verified that there are great possibilities in producing such types of symbioses.

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STUDIES ON THE MICROFLORA OF THE CURATIVE BOTTOM MUD OF THE THERMAL LAKE HÉVÍZ (W. HUNGARY)

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Actinomycetes can hardly play a part in the open water of Lake Hévíz. On the immediate surface of the bottom-mud region colonized chiefly by bacteria, however, the presence of a quantitatively considerable actinomycete fraction can be detected, which is composed, predominantly, of *Streptomyces* and *Micromonospora* species. At 20 cm depth under the mud-surface, the relative proportion of micromonosporae exceeds that of the streptomycetes. The species composition and community-structure of actinomycete populations of different horizons of the bottom mud-profile were analysed by simultaneous comparisons of our isolates with internationally recognized authentic strains of closely related species. The presence of numerous characteristic and rare species was detected. Among these a common cellulose degrader, which proved to be a new species of *Micromonospora* (*M. héviziensis* Fernandez and Szabó, 1982), another locally important cellulose-decomposer: *Streptomyces nigrifaciens*, the rare iodinebacterium: *Microbispora amethystogenes*, *Streptomyces streptomycini* first in natural habitats of Hungary, the common occurrence of *Streptomyces diastatochromogenes* strains of increased biochemical activity, the moderately thermophylic *Streptomyces thermophilus*, strains of the species *Streptomyces antimycoticus*, *S. antibioticus*, *S. viridochromogenes*, etc., and of *Micromonospora megalomicea*, *M. carbonacea*, *M. purpureochromogenes*, etc. The "river-lake"-character of the Lake Hévíz is also shown by the results of the bacteriological analysis of its bottom mud. In general, actinomycete communities of river-muds are predominated by streptomycetes and those of true lake-muds by micromonosporae. The mud of Lake Hévíz is colonized by a mixed actinomycete-flora composed of many streptomycetes and micromonosporae in different relations according to the depth under the mud surface horizon.

Introduction

Thermal Lake Hévíz located west of Lake Balaton, at a distance of 5.5 km from Keszthely is, with an area of 47 500 m² and a natural, curative, advantageously slightly radioactive thermal water, fed by thermal springs, from a medicinal point of view one of the most important curative watering places in Central Europe. Its temperature is 33–35 °C in summer and never falls below 26 °C during the year. Its water is drained off through a channel, so the total water body of the lake can be exchanged every 24 hours. Its bottom deposit used extensively for curative purposes, is 1–2 m thick, it contains organic matters of plant origin, deriving from the peat layer surrounding the lake. The organic matter mainly consists of humin + lignin (4.79%), humic acids (1.27%), cellulose (0.4%), hemicellulose (1.63%), furthermore of soluble (0.9%) and native, undecomposed (0.9%) organic matters. Na^+ (0.184 g/1000 g mud), Ca^{2+} (1.52 g), Mg^{2+} (0.316 g), SO_4^{2-} (3.226 g), HCO_3^- (2.27 g) and H_2SiO_3 (0.03 g; CSAJÁGHY 1949) play an important part in the inorganic fraction of the mud. The alkaline mud (pH 7.8), which is rich in sulphur (total sulphur 0.51%), dominated by calcium-magnesium carbonate and sulphates also contains oestrogen matters with hormone activity (GYIMÓTHY 1970). One

can get to know the physicochemical conditions and geology of the lake better from the works of SCHULHOF (1957), PLÓZER (1976), etc. Unfortunately the particular bacterial communities of the water and bottom mud, respectively, of the lake are hardly or not at all known. In the course of my study-tour to Hungary I intended to retrieve these shortcomings with my modest data.

Material and method

The samples were collected by the divers of the Amphora Light-Divers' Sport Club under aseptic circumstances, farther from the crater (largest thermal spring) from a region of the lake where the water depth was about 3 m, then they were delivered in sterile Erlenmeyers to the laboratory within the shortest time, in order to avoid changes in germ numbers. Essentially, four horizons of the lake profile have been sampled:

I. Lake water — 20 cm above the mud-surface,

II. Mud-surface — the 1–2 cm deep layer of the bottom,

III and IV. Mud — 20 and 60 cm, respectively, below the bottom surface.

For isolating and counting bacteria others as actinomycetes the following media were used: nutrient-agar (Difco), starch-agar (starch 10 g, peptone 5 g; meat extract 3 g; agar 15 g; distilled water 1000 ml; pH 7.0), synthetic sodium propionate-cycloheximide-tiamine-agar (KH_2PO_4 0.466 g; Na_2HPO_4 0.732 g; KNO_3 0.1 g; NaCl 0.29 g; $MgSO_4 \cdot 7\ H_2O$ 0.1 g; $CaCO_3$ 0.02 g; Na-propionate 0.2 g; $FeSO_4 \cdot 7\ H_2O$ 200 μg; $ZnSO_3 \cdot 7\ H_2O$ 180 μg; $MnSO_4 \cdot 4\ H_2O$ 20 μg; agar 18 g; distilled water 1000 ml; cycloheximide 50 mg; tiamine HCl 40 mg; the latter two reagents were sterilized by filtration), while for isolating and counting actinomycetes three further media were used: starch casein-agar (starch 10 g; casein 1 g; K_2HPO_4 0.5 g; agar 15 g; distilled water 1000 ml; pH 7.0–7.5), starch-agar and sodium propionate-agar. (See FERNANDEZ and SZABÓ, I. M. 1978, FERNANDEZ 1980, FERNANDEZ and SZABÓ, Zs. 1982.) Plates were inoculated superficially. Incubation took place at 30 °C in dark, for 3–14 days. Isolation was carried out on a non-selective (random) basis. The appeared colonies of actinomycetes were transferred on oat-meal and on yeast-extract starch-agar slants. Only actinomycete isolates were investigated in detail. Pure cultures were obtained by repeated spreadings and reisolations. Morphological, physiological and biochemical diagnostic properties of the isolated strains which proved to be the members of the genera *Streptomyces*, *Micromonospora*,

Table 1

Number of the platable aerobe and facultative anaerobe bacteria and actinomycetes in 1 ml of the open water and bottom-mud, respectively, of Lake Hévíz

(Sampling: February 4, 1979)

	Total germ-number estimated using nutrient-agar as plating medium after an incubation for 4 days	Total number of actinomycetes. Plating medium: starch casein agar. Incubation for 7 days	Starch agar (incubation for 7 days)		Na-propionate cycloheximide-agar (incubation for 14 days)	
			Bacteria	Actino-mycetes	Bacteria	Actino-mycetes
Lake water (20 cm above mud-surface)	4.8×10^3	0	4.1×10^3	0	2.7×10^3	0
The uppermost layer of the sediment	2.7×10^5	3.6×10^4	1.0×10^6	1.0×10^5	2.9×10^5	3.2×10^4
Lake sediment (20 cm under mud-surface)	2.2×10^4	1.8×10^3	4.7×10^5	2.8×10^4	4.6×10^3	8.6×10^3
Lake sediment (60 cm under mud-surface)	3.8×10^4	1.3×10^3	2.4×10^5	4.0×10^3	3.0×10^4	2.6×10^3

etc. were tested according to international standards, using the routine methods employed' generally, in the Department of Microbiology of the ELTE (GOTTLIEB and SHIRLING 1970, PRIDHAM and TRESNER 1974, SZABÓ, Zs. 1981, etc.). The isolated *Streptomyces* strains were clustered by us in larger similarity-groups (species) according to the characteristics of the International Streptomyces Project (ISP, SZABÓ and MARTON 1976). Other actinomycete strains which were identified as members of other genera were described and differentiated according to diagnostic characteristics and methods offered by different workers dealing with these genera (see FERNANDEZ and SZABÓ, Zs. 1982, FERNANDEZ 1980, SZABÓ, Zs. 1981). Strains were identified partly by direct comparisons based on synchronous investigations with closely related authentic strains obtained from international culture-collections partly by using diagnostic keys given later. Isolated strains of documentation value were deposed in the culture-collection of Department of Microbiology of ELTE.

Results

Table 1 illustrates the germ-number distributions in relation of different plating media and habitat-samples. The total number of bacteria, apart from one sample, exceeded in each case and on each plating medium that of the actinomycetes. In water samples actinomycetes could not be found at all, from which the conclusion may be drawn that they are not members of the bacterioplankton, but adhere firmly to the surfaces of mud-particles. The greatest population density was shown in the relation of both bacteria and actinomycetes in the area of the mud-free-water interfaces. At a depth of 20 cm of the sediment the number of aerobe and facultative organisms was already considerably reduced and this decreasing tendency in the population density could also be observed in the samples deriving from a depth of 60 cm, at least using starch-agar as plating medium. In the water/mud border-area 10% of the platable microflora was constituted by actinomycetes. The relative number of the latter gradually decreased with increasing depth, namely to 6% at 20 cm and to 1.6% at 60 cm. As the mud can be hardly homogenized for plating and the hyphal filaments of actinomycetes cannot be disintegrated into cell-equivalent units, it can be supposed that on the sediment surface the fraction of these organisms may exceed 50% of the microflora. The distribution at generic level of the isolated and studied strains is shown in Table 2. Most of them derived from the surface of the bottom mud. Among them 1 *Micropolyspora*-, 24 *Micromonospora*-, and 149 *Streptomyces*-strains occurred. The number of streptomycetes decreased quickly with increasing depth, and in a depth of 20 cm the actinomycete fraction was already dominated by

Table 2

Number and distribution at generic level of actinomycete strains isolated from the bottom-sediment of Lake Hévíz and studied

Genus	Habitats from which the strains derive			
	Lake water	Immediate surface of the bottom-mud	Mud-matter 20 cm under the mud-surface	Mud-matter 60 cm under the mud-surface
Streptomyces	0	149	33	25
Micromonospora	0	24	42	16
Nocardia	0	0	1	1
Microbispora	0	0	1	0
Micropolyspora	0	1	0	0

Table 3

Description of selected, representative Streptomyces

Strain number	Species	Sporophore	Spore ornamentation (elektr. opt.)	Spore-mass colour group according to TRESNER and BACKUS	Colour series of vegetative mycelium
II-26	*S. nigrifaciens*	RF	Sm	G	Y-B
II-198	*S. nigrifaciens*	RF	Sm	G	Y-B
III-70	*S. nigrifaciens*	RF	Sm	G	Y-B
II-104	*S. parvus*	RF	Sm	Y	Y-B
II-75	*S. parvus*	RF	Sm	Y	Y-B
II-195	*S. parvus*	RF	Sm	Y	Y-B
IV-41	*S. parvus*	RF	Sm	Y	Y-B
II-53	*S. diastatochromogenes*	S	Sm	G	Y-B
II-164	*S. diastatochromogenes*	S	Sm	G	Y-B
III-49	*S. diastatochromogenes*	S	Sm	G	Y-B
II-20	*S. diastatochromogenes*	S	Sm	G	Y-B
II-151	*Streptomyces* sp. (*endus?*)	S	Sm	G	Y-B
II-18	*Streptomyces* sp. (*endus?*)	S	Sm	G	Y-B
II-134	*Streptomyces* sp. (*endus?*)	S	Sm	G	Y-B
II-95	*Streptomyces* sp. (*endus?*)	S	Sm	G	Y-B
II-153	*S. parvulus*	S	Sm	G	Y-B
II-42	*S. parvulus*	S	Sm	G	Y-B
IV-32	*S. parvulus*	S	Sm	G	Y-B
II-25	*S. parvulus*	S	Sm	G	Y-B
II-98	*S. galilaeus*	S	Sm	G	Y-B
II-170	*S. oligocarbophilus*	RF	Sm	Y	Y-B
IV-4	*S. oligocarbophilus*	RF	Sm	Y	Y-B
III-10	*S. violaceoruber*	S	Sm	GB	Y-B + B-R
IV-7	*S. violaceoruber*	S	Sm	GB	Y-B + B-R
II-34	*S. anandii*	S	Sm	R	Y-B
IV-20	*S. anandii*	S	Sm	R	Y-B
III-4	*S. olivaceus*	RF	Sm	G	Y-B
IV-54	*S. galbus*	S	Sm	G	Y-B
IV-28	*S. antimycoticus*	RF	Sp	G	Y-B
II-162	*S. antimycoticus*	RF	Sp	G	Y-B
II-146	*S. viridochromogenes*	S	Sp	B	Y-B
II-66	*S. thermophilus*	RF	Sp	G	Y-B
II-33	*S. tanashiensis*	RF	Sm	G	Y-B
IV-47	*S. bluensis*	S	Sp	B	Y-B
II-252	*S. tetanusemus*	RF	Sm	Y	Y-B
II-55	*S. streptomycini*	RF	Sm	Y	Y-B
II-90	*Streptomyces* sp. (*antibioticus?*)	RF	Sm	G	Y-B
II-21	*S. spadicis*	RF	Sm	G	Y-B
II-113	*S. antibioticus*	RF	Sm	G	Y-B
II-67	*S. ganmycicus*	S	Sp	G	Y-B
II-29	*S. roseoviridis*	RF	Sm	R	Y-B
II-68	*S. lavendulae*	S	Sm	R-G	Y-B

* Abbreviations: RF = Rectus-flexibilis; S = Spiral; Sm = not ornamented, smooth; Sp = spiny ornamentation (at an enlargement of 4000 times); Y-B = colour series of yellowish-brown endopigmentation; Y-B + B-R = the substrate mycelium pigment is pH sensitive, changing from blue to red; G = spore mass colour: Gray-series; Y = spore mass colour: Yellow-

*strains isolated from the mud of Lake Hévíz**

Melanoid pigment		Utilization as sole source of carbon on PRIDHAM and GOTTLIEB's synthetic basal medium											
M6	M7	D-Glucose	L-Arabinose	Sucrose	D-Xylose	i-inositol	D-Mannitol	D-Fructose	Rhamnose	Raffinose	Without C-source	Cellulose hydrolysis	Starch hydrolysis
—	—	+	+	—	+	—	+	+	+	—	—	+	+
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series; R = spore mass colour: Red-series; B = spore mass colour: Blue-series; GB = Grayish blue; RG = reddish-gray: D = questionable, uncertain utilization; M6 = Iron peptone agar; M7 = Tyrosine agar.

Table 4

Comparison of selected representative strains of Micromonospora isolated recognized Micromonospora spp. on the basis of

Number designation of strains	Species	C-source utilization spectra												
		D-Glucose	L-Arabinose	D-Xylose	L-Rhamnose	D-Fructose	D-Mannose	D-Galactose	D-Lactose	Sucrose	D-Melibiose	Trehalose	L-Melicitose	Raffinose
III-a	*M. heviziensis*	+	+	+	+	+	+	+	+	+	+	+	+	+
II-176	*M. heviziensis*	+	+	+	+	+	+	+	+	+	+	+	+	+
III-126	*M. heviziensis*	+	+	+	+	+	N	+	+	+	+	+	+	+
III-129	*M. heviziensis*	+	+	+	+	+	+	+	+	+	+	+	+	+
IV-29	*M. heviziensis*	+	+	+	+	+	+	+	+	+	+	+	+	+
III-84	*M. megalomicea*	+	+	+	—	+	N	?	—	+	—	+	—	—
III-86	*M. megalomicea*	+	+	+	—	+	+	?	+	+	—	+	—	—
III-87	*M. megalomicea*	+	+	+	—	+	+	?	?	+	—	+	—	—
II-64	*M. carbonacea*	+	+	+	—	+	N	+	+	+	+	+	—	—
II-194	*M. carbonacea*	+	+	+	—	+	+	+	+	+	+	+	—	—
II-25	*M. carbonacea*	+	+	+	—	+	+	+	+	+	+	+	—	—
III-33	*M. carbonacea*	+	+	+	—	+	N	+	+	+	+	+	—	—
III-94	*M. carbonacea*	+	+	+	—	+	+	+	+	+	+	+	—	—
II-80	*M. purpureochromogenes*	+	—	+	—	+	+	+	+	+	+	+	—	+
II-185	*M. purpureochromogenes*	+	+	+	—	+	+	+	+	+	+	+	—	?
II-204	*M. purpureochromogenes*	+	+	+	—	+	+	+	+	+	+	+	—	+
IV-46	*M. purpureochromogenes*	+	—	+	—	+	+	+	+	+	+	+	—	+
II-30	*M. chalcea*	+	+	+	—	+	N	+	+	+	+	+	+	+
II-131	*M. chalcea*	+	+	+	—	+	N	+	+	+	+	+	—	+
III-31	*Micromonospora* sp. (*narashinoensis?*)	+	—	+	—	+	+	+	+	+	+	+	—	—
III-32	*Micromonospora* sp. (*narashinoensis?*)	+	—	+	—	+	+	+	+	+	+	+	—	—
II-79	*Micromonospora* sp. (*narashinoensis?*)	+	+	+	—	+	N	+	+	+	+	+	—	—
IV-1	*M. coerulea*	+	+	+	?	+	+	+	+	+	+	+	—	+
ATCC 27358	*M. parva*	+	+	+	—	+	+	+	+	+	+	+	—	—
ATCC 21773	*M. inositola*	+	+	+	—	+	+	+	+	+	+	+	—	+
ATCC 27029	*M. aurantiaca*	+	+	+	—	+	+	+	+	+	+	—	—	+
ATCC 12452	*M. chalcea*	+	+	+	—	+	+	+	+	+	+	+	—	+
ATCC 27114	*M. carbonacea*	+	+	+	—	+	+	+	+	+	+	+	—	—
ATCC 27596	*M. halophytica* ssp. *halophytica*	+	+	?	—	+	+	+	+	+	+	+	—	—
ATCC 27331	*M. narashinoensis*	+	+	+	—	+	+	+	+	+	+	+	—	+
ATCC 27600	*M. inyoensis*	+	—	—	—	+	+	+	—	+	—	+	—	—
ATCC 27598	*M. magalomicea* ssp. *nigra*	+	+	+	—	+	+	—	+	+	—	+	—	—
ATCC 21826	*M. sagamiensis*	+	+	+	—	+	+	+	—	+	—	+	—	—
ATCC 27007	*M. purpureochromogenes*	+	—	+	—	+	+	+	+	+	+	—	—	+
ATCC 27334	*M. brunnea*	+	—	+	—	+	+	+	+	+	+	—	—	+
ATCC 27008	*M. coerulea*	+	—	+	—	+	+	+	+	+	+	+	—	+
ATCC 21819	*M. olivoasterospora*	+	—	+	—	+	+	+	—	+	—	+	—	—
ATCC 15835	*M. purpurea*	+	+	+	—	—	+	—	—	+	—	+	—	—
ATCC 15836	*M. echinospora* ssp. *ferruginea*	+	+	+	+	—	+	—	—	+	—	+	—	—
ATCC 15837	*M. echinospora* ssp. *echinospora*	+	+	+	+	—	+	—	—	+	—	+	—	—
ATCC 27030	*M. lilacina*	+	+	+	+	+	+	+	+	+	+	+	—	+
ATCC 27031	*M. rubra*	+	+	+	+	+	+	+	+	—	+	+	—	+

Abbreviations: + = strong growth, positive utilization; +D = weak growth; — = no growth

from the mud of Lake Hévíz with authentic strains of internationally physiological characteristics of diagnostic value

D-Mannitol	i-inositol	Dulcitol	Glycerol	Dextrine	Without C (basal medium)	Cellulose-decomposition	Milk digestion (on agar plates, in mm	Gelatine hydrolysis (on agar plates, in mm)	NaCl tolerance (%)				pH tolerance					Growth at °C			
									1.5	3.0	4.5	5.0	4.5	5.0	6.0	7.0	8.0	37 °C	40 °C	50 °C	55°C
+	+	—	—	+	—	+	17	20	+	—	—	—	—	+	+	+	?	—	—	—	—
+	+	—	—	+	—	+	20	20	+	?	—	—	?	+	+	+	+	—	—	—	—
+	+	?	—	N	—	+	10	20	+	—	—	—	—	+	+	+	—	—	—	—	—
+	+	—	?	+	—	+	20	20	+	—	—	—	—	?	+	+	—	—	—	—	—
+	+	—	—	+	—	+	15	22	+	—	—	—	—	+	+	+	+	—	—	—	—
—	—	—	—	N	—	+	25	20	+	+	+	?	—	—	+	+	+	+	+	—	—
—	—	—	—	+	—	+	25	21	+	+	+	?	—	—	+	+	+	+	+	—	—
—	—	—	—	+	—	+	25	25	+	+	+	—	?	?	+	+	+	+	+	—	—
—	—	—	—	N	—	+	15	21	+	?	—	—	—	+	+	+	?	+	+	—	—
—	—	—	—	+	—	+	15	N	N	N	N	N	N	N	N	N	N	+	+	—	—
—	—	—	—	+	—	+	17	25	+	+	—	—	—	+	+	+	—	+	+	—	—
—	—	—	—	N	—	+	15	23	+	+	—	—	—	+	+	+	+	+	+	—	—
—	—	—	—	+	—	+	15	25	+	—	—	—	—	+	+	+	+	+	+	—	—
—	—	—	+	+	—	—	17	22	+	—	—	—	—	+	+	+	?	+	+	—	—
—	—	—	+	+	—	—	8	13	+	—	—	—	—	+	+	+	?	+	+	—	—
—	—	—	+	+	—	—	15	21	+	—	—	—	—	+	+	+	—	+	+	—	—
—	—	—	+	+	—	+	13	25	+	—	—	—	—	+	+	+	+	+	+	—	—
—	—	—	+	N	—	—	20	20	+	—	—	—	—	+	+	+	—	+	+	—	—
—	—	—	+	N	—	—	20	N	+	—	—	—	—	+	+	+	?	+	+	—	—
—	—	—	—	+	—	—	10	22	+	—	—	—	—	+	+	+	+	+	+	—	—
—	—	—	—	+	—	—	10	27	+	—	—	—	—	+	+	+	?	+	+	—	—
—	—	—	—	N	—	—	10	20	+	—	—	—	—	?	+	+	?	+	+	—	—
—	+	—	—	+	—	—	15	15	+	—	—	—	—	+	+	+	?	—	—	—	—
—	—	—	—	+	—	+	21	20	+	+	—	—	—	?	?	+	+	+	+	—	—
—	+	—	—	+	—	—	20	23	+	—	—	—	—	+	+	+	+	+	+D	—	—
—	—	—	—	+	—	—	8	13	+	+	+	—	—	?	+	+	+	+	+	—	—
—	—	—	—	+	—	+	26	25	+	+	?	—	—	+	+	+	+	+	+	—	—
—	—	—	—	+	—	+	26	0	+	+	—	—	—	?	+	+	+	+	+	—	—
—	—	—	—	+	—	+	18	20	+	+	—	—	—	—	+	+	+	+	+	—	—
—	—	—	—	+	—	?	24	20	+	+	+	+	—	+	+	+	+	+	+	—	—
—	—	—	—	+	—	—	26	26	+	+	—	—	—	—	+	+	?	+	N	—	—
—	—	—	—	+	—	+	23	19	+	+	?	—	—	—	?	+	+	+	—	—	—
—	—	—	—	+	—	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
—	—	—	+	+	—	—	7	16	+	—	—	—	—	+	+	+	?	+	+	—	—
—	—	—	+	+	—	+	12	25	+	+D	—	—	—	?	+	+	—	+	+	—	—
+	—	—	—	+	—	—	N	N	+	—	—	—	—	?	+	+	—	+	+	—	—
—	—	—	—	+	—	—	0	27	+	+	—	—	—	+	+	+	—	+	+	—	—
—	—	—	—	+	—	+	20	18	+	+	—	—	—	—	—	+	?	+	+	—	—
—	—	—	—	+	—	+	25	18	+	+	—	—	—	—	+	+	?	+	+	—	—
—	—	—	—	+	—	+	25	17	+	?	—	—	—	—	+	+	?	+	+	—	—
+	+	—	+	+	—	?	17	17	+	—	—	—	?	?	+	+	?	+D	+	—	—
+	+	—	+	+	—	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N

or utilization; ? = uncertain results; N = undetermined.

Micromonospora. At this depth the presence in low number of *Nocardia* and *Microbispora* was also detected. It is interesting that at a depth of 60 cm, where the population density also of *Micromonospora* already strongly decreases, relatively many *Streptomyces* can be still isolated. In our opinion these are germinating from inactive spores. At identifying the isolated *Streptomyces* strains we relied on the diagnostic key elaborated by us (SZABÓ et al. 1975), on the taxonomic work of PRIDHAM and TRESNER (BERGEY's Manual, 1974), the ISP-redescriptions, HÜTTER's monograph (1967), and on the results of direct comparisons with authentic, internationally recognized strains. From among the 207 isolated *Streptomyces* strains 175 could be identified. The distribution at species level of these is as follows. *Streptomyces nigrifaciens* 22; *S. parvus* 12; *S. diastatochronogenes* 22; *Streptomyces* sp. (*endus*?) 20; *S. parvulus* 19; *S. galilaeus* 8; *S. oligocarbophilus* 8; *S. violaceoruber* 6; *S. anandii* 6; *S. olivaceus* 6; *S. galbus* 6; *S. antimycoticus* 4; *S. viridochromogenes* 4; *S. thermophilus* 4; *S. tanashiensis* 4; *S. bluensis* 3; *S. tetanusemus* 3; *S. streptomycini* 3; *Streptomyces* sp. (antibioticus?) 3; *S. spadicis* 3; *S. antibioticus* 3; *S. ganmycicus* 2; *S. roseoviridis* 2; *S. lavendulae* 2. The species *S. nigrifaciens* and *S. diastatochromogenes* occurred in the greatest number. But many species occurred only sporadically. The occurrence in the mud of this lake of the moderately thermophilic *S. thermophylus*, the streptomycine-producing strains of *S. streptomycini* isolated first from natural habitat in Hungary, furthermore of *S. tetanusemus* is remarkable. Among streptomycetes obtained from the mud of Lake Hévíz there are several known antibiotic producers. Their presence cannot be left out of consideration when the biological qualification of the curative mud is made. The most commonly occurring species of *Streptomyces* in the bottom mud-surface region is *S. nigrifaciens*. All of its strains proved to be active cellulose-decomposers. This microbe together with other mud cellulose-decomposer spp. of *Micromonospora* (see below) may effectively take part in releasing radioactive elements bound to the organic fraction of the mud. A short description of some representative *Streptomyces* strains obtained from the mud of Hévíz is presented in Table 3.

Twenty-four from among the isolated *Micromonospora* strains represented a particular type of this genus, which was found at analysing the mud-community as a codominant organism and was described and introduced in the literature as a new species (*M. heviziensis*; FERNANDEZ and SZABÓ ZS. 1982). Besides these, 15 *Micromonospora megalomicea*, 8 *M. carbonacea*, 6 *M. purpureochromogenes*, 6 *M. chalcea*, 3 *M. narashinoensis* (?) and 2 *M. coerulea* strains were also identified. Their identification was carried out by means of comparative studies with authentic, mostly type-strains. Four of the 24 strains of *M. heviziensis* derived from the mud-surface region, 17 from the mud at a depth of 20 cm and 3 from a depth of 60 cm. Most of the strains of *M. megalomicea* (8), *M. carbonacea* (4), *M. narashinoensis* (3) and all of *M. coerulea*-strains derived also from a mud-depth of 20 cm. On the other hand, the species *M. purpureochromogenes* and *M. chalcea* seemed to be more frequent in the mud-surface region. Some of their selected representative strains are shown in Table 4, in which the data relating to the authentic strains used for the comparisons, on the basis of our own investigations, are given as well. Physiological characteristics used for their identification were the same as those widely used in the taxonomic work with the members of the genus *Micromonospora*. The morphological and cultural characteristics are not given here (cf. FERNANDEZ 1980). It is to be noted that e.g. in the case of the strains of *M. purpureochromogenes*, isolated from Lake Hévíz, Dr. L. KONDICS detected also the spiny surface ornamentation of spores, which is characteristic of this species, by means of electron-microscopic observations ($\times 9000$).

Most of the *Micromonospora* strains isolated from the mud of Lake Hévíz showed, together with strains of *M. heviziensis* cellulolytic activities. Presumably a strong aerobe or microaerophilic cellulose-decomposition may take place at least in the mud-surface region of the lake. Members of the genus *Micromonospora* being characteristic and common in the

Table 5

Comparison of strain III-28 of Microbispora isolated from the mud of Lake Hévíz with strain KCC-A-0021 of Microbispora amethystogenes and strain KCC-A-0023 of M. diastatica on the basis of simultaneous laboratory tests

Diagnostic properties	Number designation of strains		
	KCC A-0021	III-28	KCC A-0023
Utilization of C-sources			
D-Glucose	+	+	+
L-Arabinose	+	+	+
D-Xylose	+	+	+
Rhamnose	—	—	—
D-Fructose	+	+	+
D-Galactose	+	+	+
D-Lactose	+	+	+
Sucrose	+	+	+
D-Melibiose	—	—	+
L-Melicitose	—	—	—
Raffinose	—	—	—
D-Mannitol	+	+	+
i-inositol	?	—	+
Dulcitol	—	—	—
Glycerol	—	—	+
Without C-source	—	—	—
Growth at			
26 °C	+	+	+
30 °C	+	+	+
37 °C	+	+	+
40 °C	+	+	+
50 °C	—	—	—
NaCl-tolerance			
1.5%	+	+	+
3.0%	—	—	—
Amilolysis after 21 days	+ (6 mm)	+ (5 mm)	+ (12 mm)
Iodinine production	+	+	—
Gelatine hydrolysis after 15 days	+ (6 mm)	+ (5 mm)	+ (10 mm)
Cellulose decomposition after 60 days	+	+	+

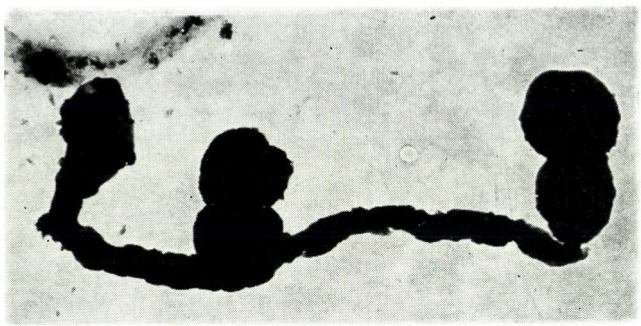

Fig. 1. Characteristic sporophores of *Microbispora amethystogenes* Nonomura et Ohara consisting of 2 spores (electronmicrograph ×12 000)

sediment of Lake Hévíz may also play an important part in generating the well-known antibacterial activity of the curative mud. We intend in the near future, together with the workers of the Research Institute of Pharmaceutical Chemistry (Budapest), to clarify this problem. Strains of *Nocardia* isolated also from the sediment could not be determined. Identification of the selected *Microbispora* strain isolated from the mud became possible only so that Dr. Akio SEINO, director of the Japanese Collection of Bacterial Strains (KCC), put the type-strain (KCC A-0021) of *Microbispora amethystogenes* and the authentic strain KCC A-0023 of *Microbispora diastatica* at our disposal. The results of their comparisons are shown in Table 5, which proves that *Microbispora amethystogenes* Nonomura et Ohara, this rare species occur in the mud of Hévíz and at the same time it could be isolated for the first time in Central Europe. The electronmicrograph (×12 000) of characteristic sporofores of our isolate (III-28) consisting of only 2 spores is shown in Fig. 1. This species, which can form bronze-violet needle-like crystals of iodinine on certain media may be otherwise a particular member of the bacterial population of the Hévíz-mud. On oat-meal agar complemented with 0.5% yeast-extract strain III-28 develops light-pink aerial mycelium, produces diffusible yellow exopigment and in the immediate vicinity of its colonies in the medium violet coloured iodinine crystals accumulate. Such crystals occur in extremely large numbers near the colonies growing on the basal medium used for carbon-source utilization tests in the presence of glucose and D-mannite. The role of iodine in the metabolism of *Microbispora amethystogenes* and the way in which this species can influence the cycling of iodine in lake muds have not yet been known. Unfortunately, we could not solve the problem of identification at species level of the *Micropolyspora* strain isolated.

Discussion

On the basis of our results it seems to be likely that actinomycetes play an important part in the mud-bacterium community of Lake Hévíz. Although their number estimated by plating on media of different composition is at most 10% of the total aerobe and facultative mud-microflora, the relative proportion of their fraction in the local bacterial biomass is presumably much larger as their hyphal structures which are hard to desintegrate may greatly reduce their platable germ-number. The actinomycete community of the mud is constituted chiefly by *Streptomyces* and *Micromonospora* species capable of

producing important bioactive compounds used extensively in pharmaceutical practice. The otherwise most frequently occurring *Micromonospora*-type of this mud-milieu proved to be a very characteristic new species (*M. heviziensis*) not detected before in any other aquatic habitat.

As to the composition of the actinomycete-fraction of this community it differs in general from that of the actinomycete populations of the river-muds, which are extremely rich in streptomycetes but contain *Micromonospora* only in relatively low number. Such a composition is characteristic of the bottom-sediment of the River Zala (W. Hungary), which has been recently studied in detail by SUMAN (1980). From this point of view, however, the bottom-mud of Lake Hévíz cannot be considered as a true lake-mud. As the latter is characterized in general by the predominant occurrence of micromonosporae and the scattered presence of *Streptomycetes*. In the mud of Lake Balaton (W. Hungary), for example, micromonosporae are predominating among actinomycetes (Zs. SZABÓ 1981), and with the increasing distance from the mouth of River Zala towards the centre of the lake the number of streptomycetes in the mud decreases and that of micromonosporae increases (FARKAS 1982).

Thus the mud-actinomycete-community of Lake Hévíz is of a transitional character, in which the members of both genera of Actinomycetales can be found in relatively great number in the mud surface-region and also under that. This phenomenon seems to be explained by the particular hydrodynamics of the lake. The water of Lake Hévíz never becomes stagnated in the basin of the lake, but due to the continuous and rich spring-water supply and outflow through a channel, it is rapidly exchanged. The question is a kind of "river-lake", on the sediment surface of which both *Streptomycetes* and micromonosporae can find the particular microhabitats satisfying their ecological requirements. Species of both genera may play an important part not only in the transformation of inorganic and organic compounds of the bottom-milieu but also in secreting bioactive compounds into the mud and water, respectively.

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SPECIAL PROBLEMS IN STUDYING PHYTOPLANKTON ASSOCIATIONS (OCCURRENCE AND ECOLOGICAL EVALUATION OF *HYALORAPHIDIUM CONTORTUM*)

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In the course of studying planktonic alga associations in surface waters of Hungary organisms such as e.g. *Hyaloraphidium contortum* Pacher et Kors., and *H. contortum* var. *tenuissimum* Kors., a microorganism without chromatophore, pyrenoid and amidon placed in the order of Chlorococcales, that even after the most recent identification books may be ranked with the algae, are often encountered. It cannot, however, placed among the primary producer organisms (that is, functionally it is not a real algal organisms — if only those species are regarded as true algae which by means of their photosynthetizing pigments are able to produce oxygen). In the Danube this species occurs in large individual numbers (1–25 million/litre) mainly from autumn to spring. If *Hyaloraphidium contortum* and its varietas were true algae, then the chlorophyll-*a* content and the oxygen production in the water of the river at the time of sampling ought to have been higher than the values actually obtained. If this species is ranked with the true algae, then the diversity of some samples will essentially change.

Introduction

In taxonomic lists of works giving account of investigations on the phytoplanktons of lakes and rivers in Hungary taxa that are not photoautotrophic organisms or do not belong to the algae often are found. To mention only a few authors' works: Hamar (1976, 1977) discusses the taxa of *Monas cylindrica* Skuja, *M. uniguttata* Skuja, *Oicomonas mutabilis* Kent, *O. termo* (Ehr.) Kent zooflagellata and *Hyaloraphidium contortum* var. *tenuissimum* among the algae of the river Tisza. *Hyaloraphidium contortum* and its varietas were reported to be present in fish-pond materials by Hajdú (1974), in Danube samples by Hortobágyi (1973), in Lake Balaton by Padisák (1978), in the Danube by Szemes (1967), in the Tisza and its affluents by Uherkovich (1971). Hortobágyi (1973), Tamás (1975), Tóth and Padisák (1978), Uherkovich (1971) equally mention the *Planktomyces bekefii* Gim. (Caulobacteriales) when dealing with the quantitative conditions and percentage composition of alga associations.

Another example may be the taxonomic key of blue algae that Felföldy (1972) compiled of species found in Hungary, including several species placed by Häusler (1982) in the order of Schizomycetes (*Lyngbya epiphytica* Hieron = *Leptothrix epiphytica* (Migula) Schoenichen et Kalberlah, *Lyngbya ochracea* (Kg.) Thur. = *Leptothrix ochracea* (Roth) Kütz., *Oscillatoria angusta* Koppe = *Achroonema angustum* (Koppe) Skuja, *Oscillatoria profunda* Kirchn. = *Achroonema profunda* Skuja).

By giving the results of investigations related with *Hyaloraphidium contortum* we wish to point to the problems arising in studying phytoplankton associations when functionally non-true algal organisms occur in larger numbers.

In the Hungarian reach of Danube *H. contortum* and its varietas occur in masses generally every year. As an example we give below the 1979 data, which are suitable for a detailed study of the above problem.

Material and method

The water samples were taken every week at Göd (1669 river kilometres) from the surface water in the mainstream of Danube.

The quantitative examination of the phytoplankton associations was carried out with the Utermöhl method (LUND et al.). The total alga number was counted up to 1000 individuals, that is, with a 95 per cent limit of confidence chosen the accuracy of individual number estimation was ± 6 per cent. In the case of *Hyaloraphidium* we counted to 400 individuals which means an accuracy of ± 10 per cent. To identify the species of the family Thalassiosiraceae we used an electron microscope. The chlorphyll-*a* content was measured by spectrophotometer, with methanol dissolution after compression through a glass fibre filter (FELFÖLDY 1974). The potential oxygen production was determined with KNÖPP's (1960) method, by oxygen induction. (Oxygen production potential—O_2PP—under constant laboratory conditions: 4000 Lux, 20–22 °C, 24 h.) The O_2PP data are the results of measuring by Susanne TAMÁS-DVIHALLY.

In determining the diversity of phytoplankton associations (SHANNON div.) we made use of the work of HAJDÚ (1978).

Results

The quantitative trend of phytoplankton associations in the Göd reach of the Danube is shown in Fig. 1. In 1979 the individual number of the phytoplankton ranged from 300 thousand to 95 million per litre. The first major increase in individual number (10–20 million/litre) began after the recedence of the river at the end of February, in the first days of March when a rapid reproduction of the species *Stephanodiscus* and *Cyclotella* started (Table 1).* From spring to autumn, in each case a rise had passed the number of algae reached 50–60 million/litre, and on 20 September the maximum value of 95 million/litre was recorded. The phytoplankton of the river was richest in species from the beginning of July to the end of September. The number of species was the largest in the order Chlorococcales. The individual and species numbers of the planktonic alga associations considerably decreased in the last days of November, and hardly changed in winter.

In the phytoplankton of the Göd reach of Danube *Hyaloraphidium contortum* and *H. contortum* var. *tenuissimum* can be found all the year round. The latter is much more frequent, and from autumn to spring attains a particularly high individual number (in 1979 the maximum number was 25.9 million ind/l — Fig. 1). As for size and shape they are totally identical with the varietas described by KORSIKOV (1953, p. 308, Fig. 275). The colourless, tapering cells are spirally bent. The spiral mostly has more than two, sometimes 5–7 whorls,

* In Table 1 under the name *Thalassiosiraceae* spp. the following, in some cases not yet finally identified species of the family Thalassiosiraceae (SIMONSEN 1979) are included: *Cyclotella atomus* Hust., *C. cryptica* Reimann, Lewin et Guillard, *C. meneghiniana* Kütz., *C. pseudostelligera* Hust., *Stephanodiscus binderanus* (Kütz.) Krieger, *S. dubius* (Fricke) Hust. *S. hantzschii* Grun., *S. invisitatus* Hohn et Hellerman, *S. tenuis* Hust., unknown *Stephanodiscus* sp. I., unknown *Stephanodiscus* sp. II., *Thalassiosira pseudonana* Hasle et Heimdal. *Stephanodiscus invisitatus* is a species new to Hungary, *Cyclotella atomus* and *C. cryptica* are ones new to the Danube. On calculating the diversity the individual numbers of the above taxa were separately taken into account.

Table 1

Characteristic phytoplanktonic communities in the stretch of Danube at Göd in 1979

Date of sampling	III. 13.	V. 16.	VIII. 2.	IX. 20.	XI. 8.	XI. 21.
Amphora ovalis var. *pediculus* Kütz.						10
Asterionella formosa Hassal	24	244	132			10
Caloneis amphisbaena (Bory) Cleve						10
Ceratoneis arcus Kütz.						10
Cocconeis pediculus Ehr.						10
Cymbella ventricosa Kütz.						20
Diatoma elongatum (Lyngb.) Agh.		61	132	97		
D. vulgare Bory	24				40	10
Melosira granulata var. *angustissima* Müll.			66	97		
Navicula cryptocephala Kütz.	48				40	20
Nitzschia acicularis W. Smith		366	594	367	80	53
Nitzschia sp.	48	122	66			53
Thalassiosiraceae spp.*	20 336	56 890	60 052	87 539	13 117	286
Surilella ovata Kütz.						10
Synedra acus Kütz.	24	183	66	194		
S. ulna (Nitzsch.) Ehr.						10
Unknown Pennales sp. I.				97		160
Unknown Pennales sp. II.						106
Unknown Pennales sp. III.						20
Bacillariophyceae total	20 504	57 866	61 108	88 391	13 277	798
Actinastrum hantzschii Lagerh.		61	198	193		
Ankistrodesmus acicularis (A. Bt.) Kors.		183	66	193		
A. angustus Bern.	24	183	1 386	870	80	20
A. arcuatus Kors.			264			
A. longissimus var. *acicularis* (Chod.) Brunnt.			330	291	120	
A. minutissimus Kors.	24	244	264	367	40	
Chodatella quadriseta Lemm.			132			
Coelastrum microporum Naeg.			792	97		
Dictyosphaerium ehrenbergianum Naeg.				193		
D. pulchellum Wood			132	193		
Didymocystis planctonica Kors.			132	193		
D. tuberculata Kors.			132	193		
Didymogenes palatina Schmidle			132			
Franceia tenuispina Kors.			66			
Kirchneriella lunaris (Kirch.) Moeb.			66	97		
K. irregularis (G. M. Sm.) Kors.			66			
Micractinium pusillum Fresen				291		
Nephrochlamys subsolitaria (G. S. West) Kors.			66			
Oocystis borgei Snow			66	97		10
O. coronata Lemm.			132			
Pediastrum borianum (Turp.) Menegh.				97		
Scenedesmus acuminatus (Lagerh.) Chod.			330			10
S. acutus Meyen			198	97		
S. denticulatus Lagerh.				97		
S. ecornis (Ralfs) Chod.						20
S. granulatus W. et G. S. West			66			
S. intermedius Chod.			66	97		
S. quadricauda (Turp.) Bréb.			264	367	80	10
S. spinosus Chod.	24		264	97		
Unknown *Scenedesmus* sp.				97		
Schroederia setigera (Schroed.) Lemm.			66		40	

Table 1 *(continued)*

Date of sampling	III. 13.	V. 16.	VIII. 2.	IX. 20.	XI. 8.	XI. 21.
Tetraëdron caudatum var. *incisum* Lagerh.			66			
T. minimum (A. Br.) Hansg.				97		
Tetrastrum glabrum (Roll.) Ahlstr. et Tiff.			132		40	
T. staurogeniaeforme (Schoed.) Lemm.	24		66	97		
Treubaria triappendiculata Bern			66			
Unknown Chlorococcales sp. I.	264	366	620	291	160	10
Unknown Chlorococcales sp. II.	24	122	370	97		10
Unknown Chlorococcales sp. III.				97		
Chlorococcales total	384	1 159	6 996	4 896	560	90
Aphanizomenon flos-aquae (L.) Ralfs				97		
Lyngbya limnetica Lemm.			66			10
Romeria gracilis Koczw.			66			
Unknown Cyanophyta sp. I.	24	61	264		40	20
Unknown Cyanophyta sp. II.					120	10
Euglena viridis Ehr.	24					
Euglena sp.	24		66			10
Trachelomonas planctonica Swir.					40	20
T. volvocina Ehr.	24					
Mallomonas sp.	24					
Pseudokephyrion sp.	48				40	
Synura uvella Ehr.						20
Chroomonas acuta Uterm.	144	1 098	462	460	120	22
Cryptomonas erosa Ehr.	24	61		97	80	10
C. ovata Ehr.			264	193	40	
Chlamydomonas sp. I.	48	732	880	770	240	33
Chlamydomonas sp. II.	240	61	240	97		
Chlamydomonas sp. III.	24		68	97		
Chlorogonium elongatum Dang.				97		
Closterium acutum var. *variabile* (Lemm.) Krieg.				97		
Unknown Chlorophyta sp.	24			97		10
Total algae thousand ind/l	21 560	61 038	70 480	95 389	14 557	1053

and is contracted. The cells are 0.6–1.0 μm wide, and 40–70 μm long depending on how much the cell-spiral is stretched or contracted.

A comparison between Figs 1 and 2 reveals that from the end of October the chlorophyll-*a* content in the Danube water is below 15 mg/m^3, and the potential oxygen production negligibly low, which corresponds to the real number of algae (without *Hyaloraphidium*).

According to the results of 1979 investigations the average chlorophyll-*a* content of 1 million alga individuals (exclusive of *Hyaloraphidium*) was 2.00 μg. With *Hyaloraphidium* reckoned among the algae the chlorophyll-*a* content of 1 million individuals was only 0.92 μg. In November and December when the number of *Hyaloraphidium* often exceeded 10 million ind/l the amount of chlorophyll-*a* per 1 million individuals ranged between 0.16 and 0.53 μg. The average value of potential oxygen production by 1 million algae (without *Hyaloraphidium*) was 0.45 mg, while in the case of the alga number reckoned with *Hyaloraphidium* only 0.28 mg, in 1979.

Having determined the 1979 diversity of planktonic alga associations in the Göd reach of the Danube we found that from the beginning of October (when with two exceptions

the number of algae fell below 10 million ind/l, the individual number of Hyaloraphidium considerably increased) remarkable differences in diversity and uniformness were shown if we reckoned with or without the individual number of *Hyaloraphidiums*. The differences were sharpest with the samples taken at the end of November–beginning of December, since the number of algae in the Danube was then 1 million (29 November) and 300 thousand (6 December) ind/l, respectively, and the individual number of *Hyaloraphidiums* was, at the same time, 24 and 12 million per litre, respectively. (Fig. 3 — In the lower diagram of the figure the

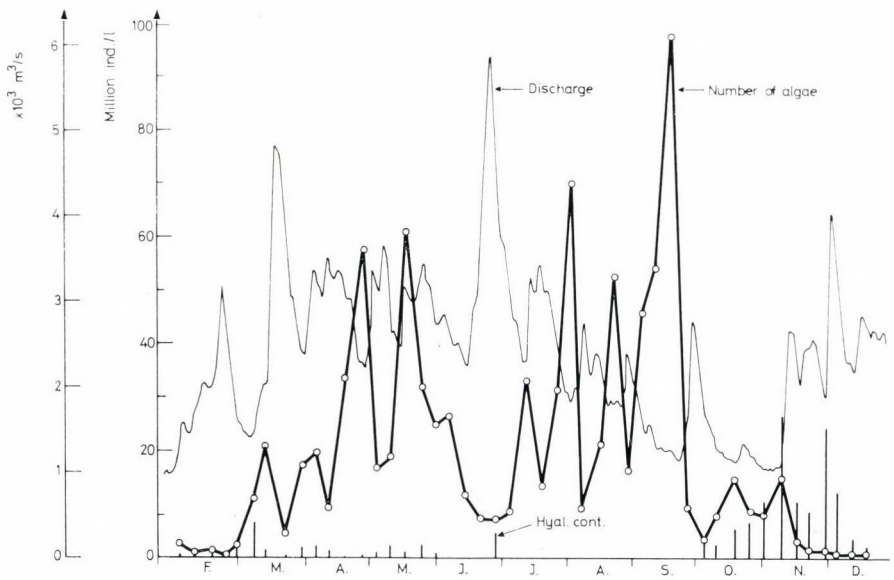

Fig. 1. Changes of the discharge, the number of planktonic algae and *Hyaloraphidium contortum* in 1979

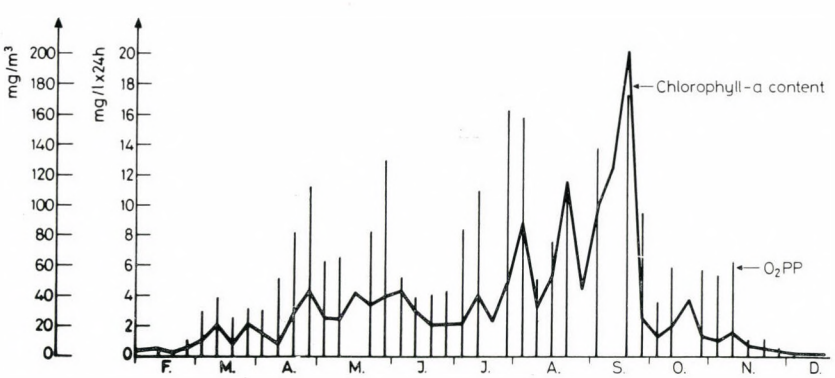

Fig. 2. Changes of the chlorophyll-*a* content and the oxygen production potential (O_2PP in 1979

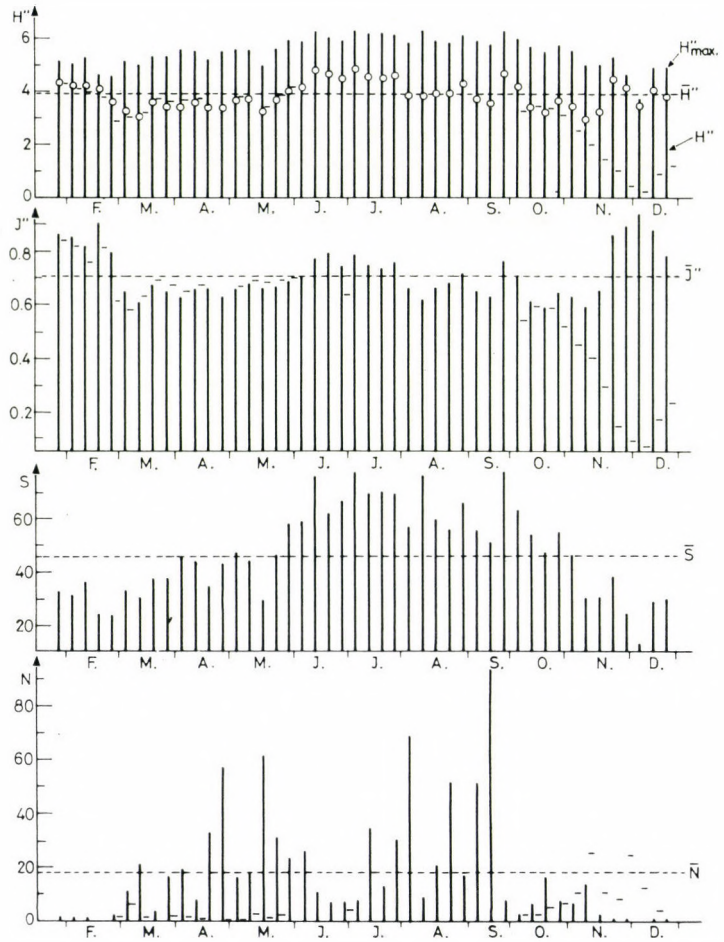

Fig. 3. Changes of the diversity (H″) and its maximum ($\log_2 s$), the evenness (J″), the species number (s — number of species/1000 individuals) and the individual number (N) in the planktonic algal communities of the Danube in 1979

individual numbers of *Hyaloraphidium contortum* and its varietas are marked with a short horizontal line. In the diversity and uniformity diagrams a similar short horizontal line is used to represent the H″ and J″ values obtained for the totalled individual numbers of *Hyaloraphidium*s and true algae, respectively.)

Discussion

The taxonomic place of *Hyaloraphidium contortum*, and of *H. contortum* var. *tenuissimum* in particular, is uncertain. It is questionable whether or not the species and its varietas are algae. They are, undoubtedly, no photoauto-

trophic organisms. The characterizations of the genus (BOURELLY 1966, FOTT 1971, KOMAREK and FOTT 1983), and particularly the description of the species and its varietas (HINDÁK 1977, KORSIKOV 1953) are not sufficiently convincing for us. Our righteous doubt is supported by the work of PRINGSHEIM (1963) who failed in growing the species or its varietas in cultures. It is not for nothing that HINDÁK (1977, p. 80), KOMAREK and FOTT (1983) consider it important —among others with *Hyaloraphidium contortum*—to produce pure cultures of the respective species, and thereby to justify them.

In our opinion the *Hyaloraphidium* and its varietas are not true algae, at least functionally not so, if we regard as true algae only those photoautotrophic organisms which by means of their photosynthetizing pigments are able to produce oxygen.

If *Hyaloraphidium contortum* and its varietas were true algae, an essentially higher chlorophyll-*a* content and potential oxygen production than those actually measured ought to have been found in the reach of Danube examined, especially in November–December 1979.

To sum it all up: in the course of studying planktonic alga associations we might make an error when taking non-photoautotrophic, not true algal organisms like *Hyaloraphidium contortum* and its varietas into account as true algae. The error will be particularly conspicuous when the individual number of the given organism is large and we compare the results of examinations to the primary production, to the processes of oxygen production, or when making statistical calculations concerning the structure of the phytoplankton association.

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OCCURRENCE OF *THALASSIOSIRA PSEUDONANA* HASLE ET HEIMDAL (BACILLARIOPHYCEAE) IN SOME RIVERS OF HUNGARY

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In the phytoplankton of the Danube, Tisza and several waters joining these rivers species of the family Thalassiosiraceae often occur in large individual numbers during the vegetation period. In the summer of 1979 the individual number of *Thalassiosira pseudonana* in the Danube reached or even exceeded 10 million per litre. Having completed the electron microscopic examination of this diatom so far unknown in Hungary we give account of differences in some morphological features in our paper. In Danube material specimens have often been found whose number of costae (measured in 1 μm) is smaller than the values given in the literature, and their costae are thicker and stronger.

Introduction

In the phytoplankton of the Danube and Tisza and in several waters joining them often large numbers of diatoms are found in the vegetation period. In periods of slow flow velocity (in receding waters or in the case of mean low water level) when the conditions are favourable for the multiplication of algae, phytoplankton blooms regularly occur (phytoplankton bloom: when the number of algae is high—several millions, to tens of millions of individua per litre). The phytoplankton bloom is characterized by the dominant presence of species of the family Thalassiosiraceae. The literary data give some information about the occurrence and quantitative conditions of the species belonging to the family Thalassiosiraceae in the above waters (Dobler and Schmidt 1980, Hamar 1976, Kiss 1974, 1975, Kiss and Szabó 1975, Schmidt and Vörös 1981, Szemes 1962, 1964, 1966, 1971, Uherkovich 1969, 1971). In our opinion this information needs revision in many respects, because some taxa are difficult to identify without detailed electron microscopic examination.

In the present paper we wish to give account of the occurrence and morphological examination of *Thalassiosira pseudonana*. At the same time we want to give information about the frequency of this species, which is difficult to study because of its small size, occurring in the phytoplankton of the waters examined, and about the individual number in the Danube.

Material and method

In our studies we used samples taken weekly or every second week between 1979 and 1982 from the surface water in the streamline of the Danube in the section between Szob and Lórév (1598–1706 km from the mouth), in the Göd arm (1679 km), in the section between Dunaharaszti and Ráckeve of the Soroksár arm (19–44 km from the lower mouth of the arm); further, samples taken between 1968 and 1979 from the Tisza at Tiszalök (535 km from the mouth of the Danube), and from the Eastern Main Channel at Tiszavasvári and Balmaz-

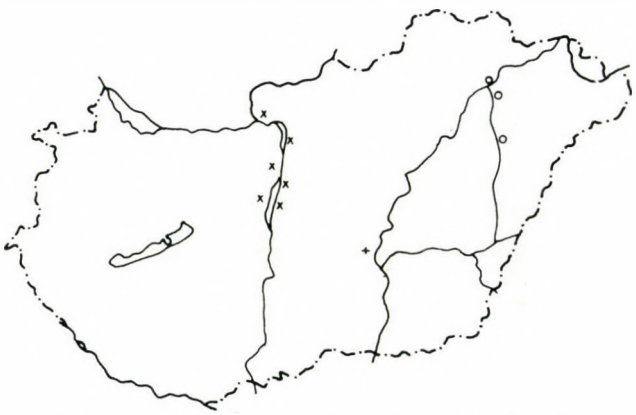

Fig. 1. Places of sampling. x — Danube, Soroksár arm; o — Tisza, Eastern Main Channel; + — Tisza, dead arm at Lakitelek

újváros (4.7 and 44.5 km, respectively, flowing out from the Tisza); and a sample series taken in May 1980 from the Lakitelek dead arm of the Tisza (Fig. 1).

The quantitative examinations were carried out with UTERMÖHL's method (LUND et al. 1958). For the electron microscope examinations the phytoplankton samples were sedimentated, then destroyed while boiled in hydrogen peroxide, and washed in distilled water. The transmission electron microscopic examinations (TEM) were performed with the Tesla BS 500 type microscope of the Department of Plant Anatomy of the Eötvös Loránd University, while the scanning electron microscope (SEM) examinations were made by the Jeol JSM-35 type microscope of the Hungarian National Geological Institute. The structural elements of the siliceous valve were measured and analysed on the basis of the papers by GENKAL (1977), GENKAL and KUZMIN (1979), and named (terminology) after ANONYMOUS (1975) and ROSS et al. (1979). In taxonomical respects SIMONSEN's (1979) work served for basis.

Results

Morphological observations

Thalassiosira pseudonana Hasle et Heimdal

(HASLE, HEIMDAL 1970, p. 565, Figs 27–38; HARGRAVES, LEVANDOWSKY 1971, p. 329, Figs 33, 34; HASLE 1976, p. 105, Figs 11–16; BELCHER, SWALE 1977, p. 293, Figs 5–7; MAKAROVA 1976, Figs 5/1–8; MAKAROVA et al. 1979, p. 923, Figs 2/1–8, 3/1–7). Synonym: *Cyclotella nana* Husted.

Morphological features visible by light microscope:

The valve diameter of round cells is larger than the pervalvar axis. The surface of valve is smooth, its structure is hardly visible. At the margin of the valve 4–13 marginal puncta are found.

With electron microscope the following can be observed:

The valve face is flat, occasionally slightly arched (Fig. 22), or its central area (the siliceous ring in valve centre and its immediate periphery) is slightly elevated (Figs 16, 18, 19). The valve diameter ranges between 2.1 and 6.6 μm. In most cases the valve is weakly silicified; on the external surface, from the valve centre to the margin thin costae run. The costae are 2–5-times dichotomously branched. In the central area of the valve a siliceous ring of irregular shape is seen, the costae start from there. On the valve margin small areolae or pores are found. The number of radial costae are 2–7 in 1 μm. On the valve margin a ring of strutted processes is seen. The number marginal strutted processes can be 3 to 13. The external tube of the marginal strutted process is longer than the internal one. Between the marginal strutted processes

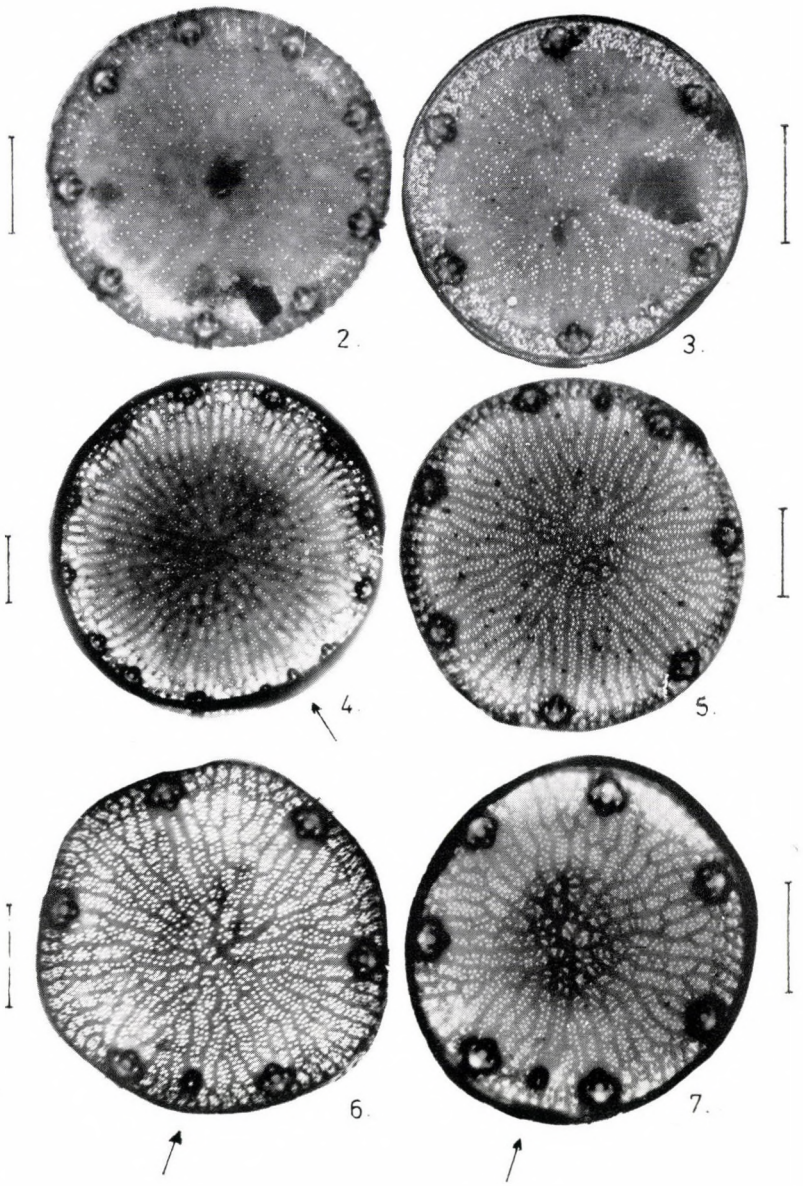

Plate 1
Structure of valve face, labiate processes marked with arrows (TEM, Scale = 1 μm). 2. Danube. 3. Tisza. 4. Danube, 5. Eastern Main Channel. 6. Tisza, 7. Eastern Main Channel

Table 1

Morphological data on Thalassiosira pseudonana

	Hasle (1976)	Belcher and Swale (1977)	Makarova et al. (1979)	Kiss (1984)
Valve diameter in μm	2.3–5	4–5	2.2–7.2	2.1–6.6
Number of costae in 1 μm	5–7		5–7	2–7
Marginal strutted processes per valve	6–15	8–13		3–13
Marginal strutted processes in 10 μm	6–14		5–12	3–9
Labiate process	1	1	1	1
Central strutted process	occasionally		x	on 1 individual

x = Usually absent on the freshwater individuals.

a small labiate process is found. (A central strutted process in the valve centre can be observed first of all on the specimens obtained from brackish water. We have recovered a single specimen only, with a central strutted process in the Danube (Fig. 21).

The above characterization largely agrees with the description by Hasle et Heimdal (1970) and with the subject in the papers of Hasle (1976), Belcher and Swale (1977), Makarova (1976), Makarova et al. (1979) (Table 1). But there are some differences and a few addenda that we want to say about by the morphological analysis of 75 EM micrographs (Table 2).

The average size of the valves is 3.8 μm. The average number of costae is 4.7 μm, that is smaller than the number in the material examined by Hasle (1976), or Makarova et al. (1979). Similarly smaller is the number of marginal strutted processes in 10 μm. We found the labiate process to be closer to one of the two marginal strutted processes in 37 specimens, and to take a symmetrical position between them in 27 specimens (Figs 12 and 7, respectively). An irregular (asymmetrical) position of the marginal strutted processes could be observed with 10 specimens (Fig. 4).

The perforations of the valve, the shape and thickness of the costae show a high variability. There is a gradual transition from the almost completely silicified, hardly perforated valves (Figs 2 and 3) to those with a considerable number of perforations (Figs 6–14). In the former ones, perforation consists of 1–2 small radially arranged pores (Figs 2 and 4), in the latter there are as much as 4–6 pores side by side, particularly in the valve margin (Figs 12–14). In some cases the pores merge into small, irregular forms of stellate appearance (Figs 8 and 9).

Intergradations can be observed between thin, lightly silicified costae (Figs 2–5) and thick, more heavily silicified ones (Figs 12–14). The number of costae and marginal strutted processes of specimens with definite, strong, thick costae differ both from the average values (Table 2) and from the specimens with thin, costae (the latter are closer to the relevant values of literature).

In specimens with thick costae the central area of the valve face is often visibly silicified (Figs 11–14). The inside silicified area can extend to 2/3 of the valve diameter (Fig. 11). Despite silicification, the costae and the irregular siliceous ring are readily visible in the valve centre (Figs 11 and 13). The dichotomous branchings of costae are fewer here than in specimens with thin costae. (Some of the specimens with thick costae resemble the small specimens of *Cyclotella pseudostelligera* Hust.)

Table 2

Data and measurements of the valve structure elements of Thalassiosira pseudonana

		Diameter μm	Number of costae in 1 μm	Number of marginal strutted processes	Number of marginal strutted processes in 10 μm
	n 62				
Individuals of typical form	min.–max.	2.1–6.6	3.2–7.4	4–13	3.4–9
	$\bar{x}$	3.767	5.484	7.707	6.477
	$S\bar{x}$	0.012	0.038	0.033	0.022
	S	0.743	1.166	1.919	1.301
	S^2	0.543	1.317	3.621	1.663
	CV	12.38	19.44	31.99	21.67
	n 13				
Individuals with thick costae	min.–max.	2.9–5.5	1.8–3.9	3–7	3–5
	$\bar{x}$	4.087	2.750	5.417	4.158
	$S\bar{x}$	0.206	0.043	0.090	0.064
	S	0.742	0.511	1.084	0.767
	S^2	0.508	0.239	1.076	0.539
	CV	18.15	8.51	18.06	12.78
	n 75				
All examined individuals	min.–max.	2.1–6.6	1.8–7.4	3–13	3–9
	$\bar{x}$	3.823	4.721	7.314	6.081
	$S\bar{x}$	0.010	0.037	0.029	0.021
	S	0.748	1.606	1.997	1.504
	S^2	0.552	2.521	3.930	2.231
	CV	12.46	26.77	33.27	25.07

n = number of data, x = mean value, $S\bar{x}$ = error of mean value, S = corrected scatter, S^2 = variance, CV = variation coefficient.

Quantitative conditions

The *Thalassiosira pseudonana* is a frequent and characteristic organism among the phytoplanktons of the Danube, Tisza and Eastern Main Channel. In every case of a phytoplankton bloom it could be observed, often in large individual numbers. To the quantitative conditions of *Thalassiosira pseudonana* we carried out detailed investigations at the Göd section of the Danube. The description below is based on the results of the 1979 investigations.

On the quantitative conditions of phytoplanktons in the Göd section of the Danube a short information has already been given (see KISS 1984, Fig. 1 and Table). *Thalassiosira*

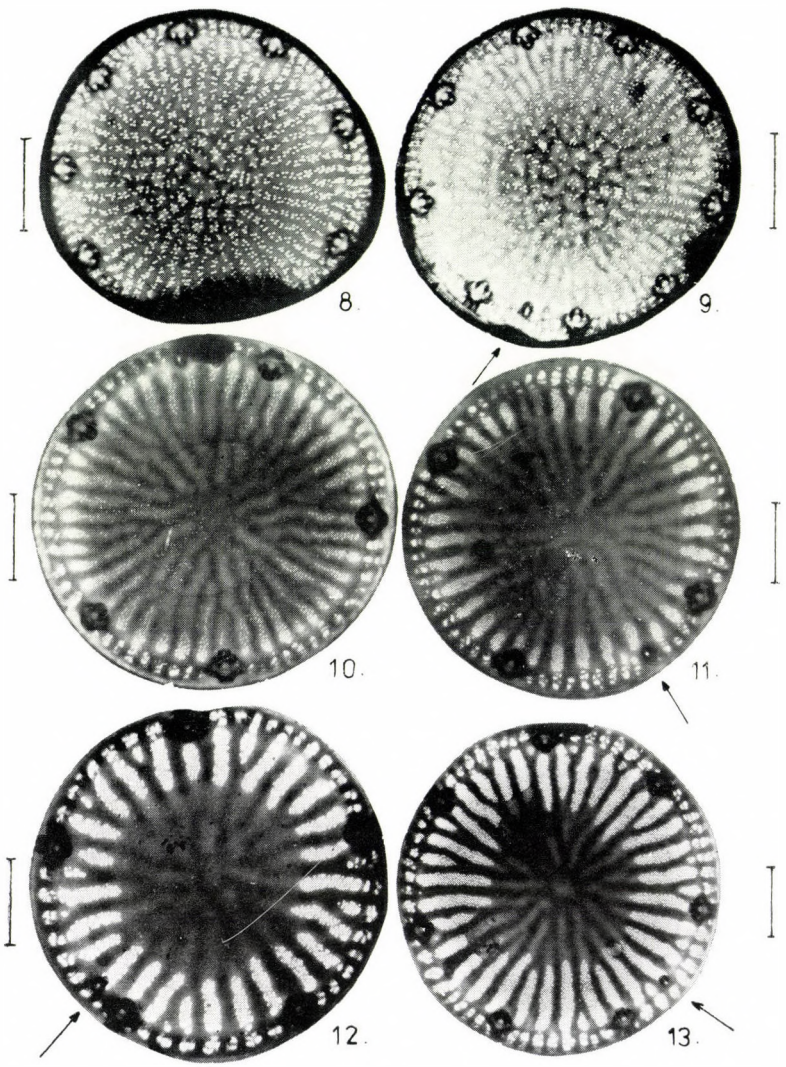

Plate 2

Structure of valve face, labiate processes marked with arrows (TEM, Scale = 1 μm). 8. Eastern Main Channel. 9. Tisza. 10–13. Danube. Valve with a labiate process asymmetrical position in 12

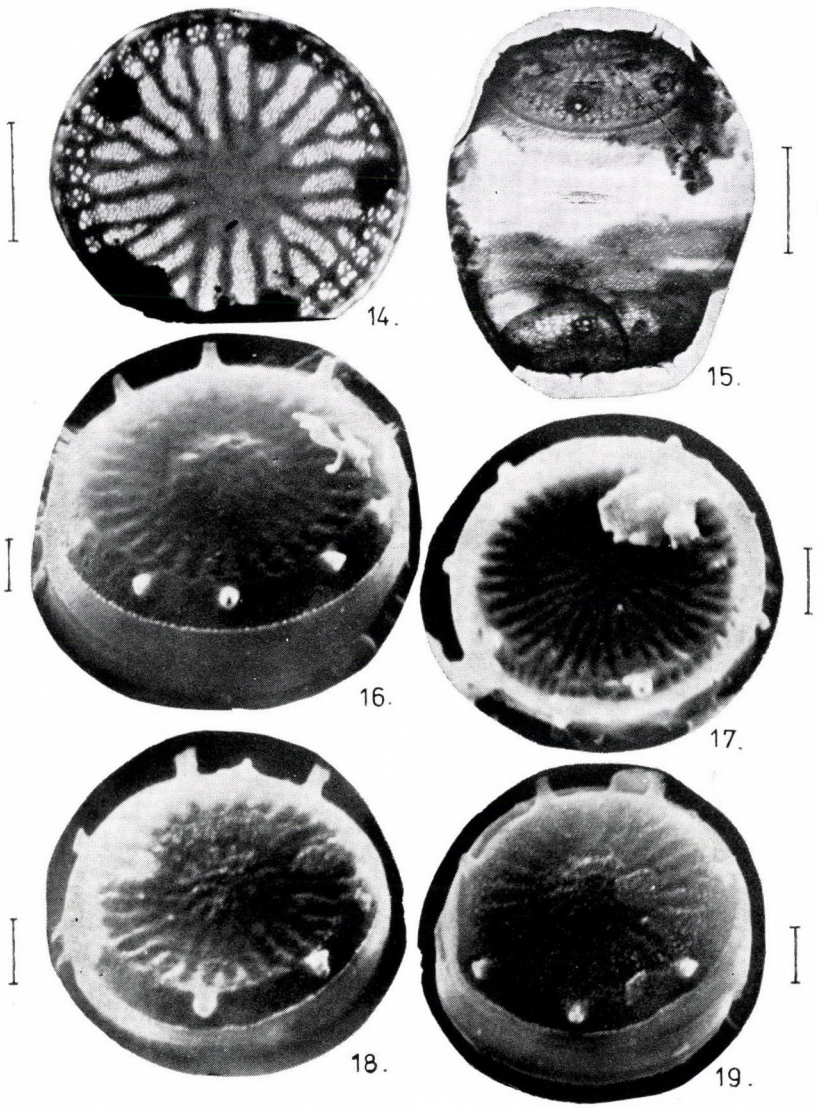

Plate 3
14. Danube (TEM) 15. Valve mantle and girdle, Tisza (TEM). 16–19. Valve face in outside view, Danube (SEM). 14–19. Scale = 1 μm

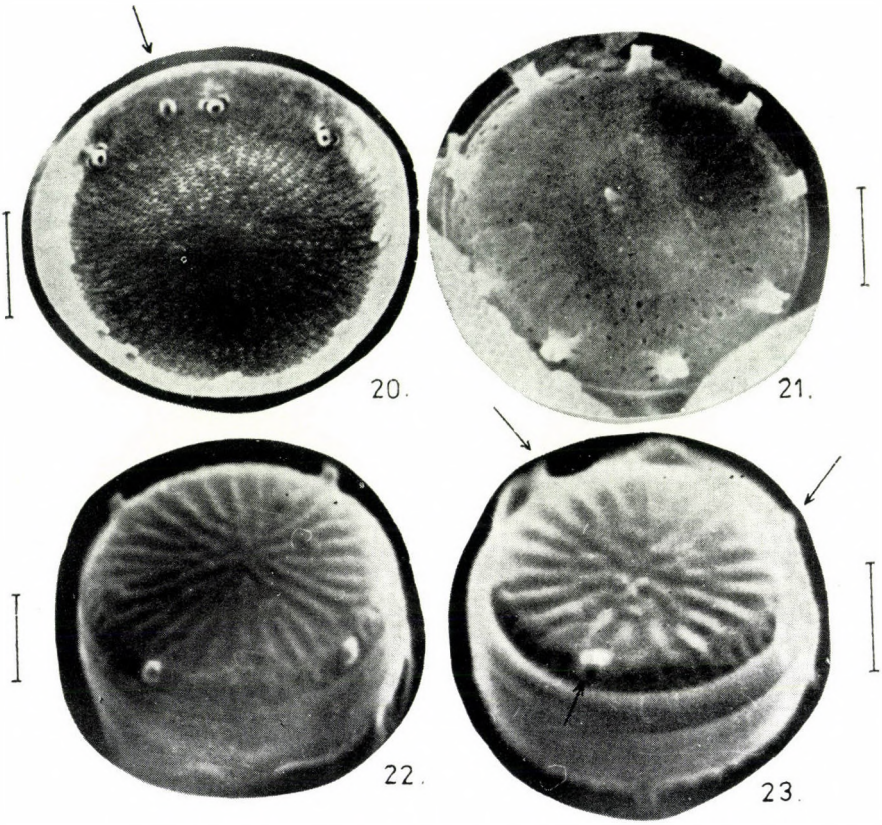

Plate 4

20. Valve face in inside view, labiate processes marked with arrows, Tisza. 21. Valve face with a central strutted process, Danube. 22–23. Dead arm of the Tisza at Lakitelek. 23. Valve with 3 marginal strutted processes (arrow). 20–23. SEM, Scale = 1 μm

pseudonana was present in the phytoplankton bloom at the beginning of March, but the individual number only ranged between 100 and 300 thousand per litre (Table 3).*

From the end of March its individual number reached or even exceeded 1 million/litre several times, and in the summer months it ranged from 5 to 10 millions. The maximum value—11.38 million/litre—was recorded on 20 September, when it represented nearly 12 per cent of the phytoplankton community.

* In Table 3 individual numbers are given separately only for *Thalassiosira pseudonana*. The name: other Thalassiosiraceae spp. (SIMONSEN 1979) covers the following, in some cases not yet finally identified, species of the family Thalassiosiraceae: *Cyclotella atomus* Hust., *C. cryptica* Reimann, Lewin et Guillard, *C. meneghiniana* Kütz., *C. pseudostelligera* Hust., *Stephanodiscus binderanus* (Kütz.) Krieger, *S. dubius* (Fricke) Hust., *S. hantzschii* Hust., unknown *Stephanodiscus* sp. I., unknown *Stephanodiscus* sp. II. For detailed data on other species of the phytoplankton association see the KISS (1984).

Table 3

Quantitative data on some phytoplankton communities in 1979 in the Göd reach of Danube

Date of sampling	18. 03.	16. 05.	02. 08.	20. 09.	08. 11.	21. 11.
Thalassiosira pseudonana	0.31	2.28	7.81	11.38	1.05	0.03
Other Thalassiosiraceae spp.	20.02	54.64	52.25	76.16	12.07	0.26
Other Bacillariophyceae	0.17	0.96	1.05	0.85	0.16	0.51
Bacillariophyceae total	20.50	57.86	61.11	88.39	13.28	0.80
Chlorococcales total	0.38	1.16	7.00	4.89	0.56	0.09
Other Chlorophyta	0.33	0.8	1.19	1.25	0.24	0.04
Cyanophyta total	0.02	0.06	0.39	0.10	0.20	0.04
Euglenophyta total	0.07		0.07			
Chrysophyceae total	0.07				0.04	0.04
Cryptomonadales total	0.17	1.16	0.72	0.75	0.24	0.03
Total number of algae, million ind/l	21.54	61.04	70.48	95.38	14.56	1.04

Discussion

In the valve-structure of *Thalissiosira pseudonana* there are intergradations between lightly perforated individuals with more perforations, resp. individuals with thin costae and those with thick ones, their taxonomic separation on the basis of examinations performed so far does not seem justified. No doubt, however, that in the literature known by us we have not encountered either the micrographs or the description of specimens with such thick costae. Strikingly enough, in more than 50 per cent of the micrographs made of Danube specimens such thick costae are seen, while in the material obtained from the Tisza and the Eastern Main Channel no such specimens occurred. This may be due to the difference in the character of water between the Danube and the Tisza, as other species of the family Thalassiosiraceae have also been found to have more fragile specimens in the Tisza than in the Danube. Here we wish to note that when examining a Danube material from an earlier collection available at our Institute (a sample taken by G. SZEMES in Budapest on 8 September 1956) we found that specimens with thick costae outnumbered the typical forms in it.

To the question why this frequent (at least in the Danube and Tisza samples of the last 15 years) diatom occurring in large individual numbers has not been detected so far in the waters of Hungary the answer is given by the small size of the species and the fine valve structure hardly visible with light microscope. Soon after the beginning of the EM examinations it was found showing the importance of the use of electron microscopes in this field of research.

According to the evidence of literary data the *Thalassiosira pseudonana* can be equally found in brackish waters and fresh waters. From experiments carried out with a Black Sea material MAKAROVA (1980) drew the conclusion that the *Thalassiosira pseudonana* is an euryhalin species.

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MONOSULCATE POLLEN GRAINS OF ANGIOSPERMS FROM HUNGARIAN ALBIAN SEDIMENTS I.

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Having studied ancient angiospermous pollen grains from the Middle Cretaceous of the Transdanubian Central Range, the authors have here described 12 new monosulcate form-species which they have assigned to four new form-genera. From the new form-genus *Crassiopollis*, 7 new form-species are described, while in the case of *Transitoripollis* n. f. gen., *Oroszlanyipollis* n. f. gen. and *Similipollis* n. f. gen. the genotype descriptions are given.

Introduction

In the last decade the origin, the time of appearance and adaptive radiation of angiosperms have been intensively studied all over the world. A host of works devoted to a re-examination of fossils that had earlier been described as angiosperms and to proving the lack of pre-Cretaceous Angiospermae evidence have been published (Hughes 1961, 1976; Wolf et al. 1975, Doyle and Hickey 1976).

As suggested by the results of research carried out this far, no angiospermous mega- or microfossils can be detected from rocks that are older than the Barremian stage of the Lower Cretaceous system. The oldest angiospermid monosulcate pollen ever found was recorded by Couper (1958), Brenner (1963), Doyle (1969) and Doyle, Drewry and Laing (1979) from Barremian sediments. Although published information on early angiospermous pollen grains from Middle Cretaceous (Aptian, Albian and Cenomanian) sediments increases from year to year, these are informative of a monosulcate pollen flora poor in species and assigned mainly to the genera *Liliacidites* Couper 1953, *Clavatipollenites* Couper 1958, and *Retimonocolpites* Pierce 1961.

The authors of the present paper, while attending the XIIth International Botanical Congress in 1975 in Leningrad, reported on a rich monosulcate angiospermid pollen assemblage with a number of new species recovered from the Albian of Hungary. The description of the new species, however, has been delayed up to the present time. In the meantime three works were published which contained in part the documentation of these as well (Juhász et Góczán 1976, Császár 1976, Juhász 1983).

The Middle Cretaceous formations containing the monosulcate pollen species here described were analyzed many-sidedly, and geologically interpreted in detail, by J. Fülöp (1975), G. Császár (1976, 1978) and Császár and Haas (1979). A brief account of the particular formations and their chrono- and palynostratigraphic subdivisions are given in the work of M. Juhász (1983).

In the following work the authors wish to describe additional Albian to Cenomanian mono- and trichotomonosulcate species, to discuss the status of the genera involved and their biostratigraphic value and then to present their proposal as to the systematic classification of these forms.

Systematic description

The morphological and structural characteristics used for the specification and systematic assignment of the mono- and trichotomonosulcate grains to be described hereinafter are assignable to three groups:

a) Definitive features which cannot be determined by measurement or calculations in a direct way, and which thus have to be assessed in descriptive conceptual terms such as shape, contour, character of sulcus, surface sculpture, structure of exine, nexine and sexine, denomination of sculptural and structural elements, etc.

For these, ERDTMAN's (1952) terminology has been used, as a rule, for the ones that can be assessed by a light microscope, while in electron microscopical descriptions of the exine structure the nomenclature proposed by WALKER (1974) has been adopted. In a few exceptional cases notions different from these have been used, for which the reader should consult KREMP (1965).

b) Measured features which can be measured by a light microscope directly on the grain or in an indirect way on electron microscopic images. These are: size, length, width, height, thickness, diameter, the spacing of two elements, etc. The value to be given may be a concrete number or a general size indication such as small (= up to 20 μ), fair (= 20–40 μ) or large (above 40 μ).

c) Calculated features that can be inferred from measured data. These include the various ratios such as the *length-width (P/E), the greatest diameter-wall thickness (P/e), the sexine-nexine (s/n), the diameter-radius (d/r), the diameter versus lumen-diameter of reticulum (P/re) ratios* or, after the division is carried out, the respective index numbers *P/E*, *P/e*, *S/n*, *d/r* and *P/re*.

The numerical data of the measured and calculated features are usually listed after the "*Diagnosis*", under the heading "*Size characteristics*". In the diagnose only size characteristics considered to be specific are quoted.

From Formations of Albian and Lower Cenomanian age only a part of the monosulcate pollen grains are described which the authors, in the light of their experience, consider to derive from angiospermid plants.

Anteturma: POLLENITES R. Pot. 1931

Turma: *Archaeoangiospermae* **nov. turma**

Subturma: Crassinexines — **nov. subturma**

Infraturma: C r a s s i n e x i n e s - n o n r e t i c u l a t i nov. infrat.

Subinfraturma: Crassinexines — nonreticulomonsulcati nov. subinfraturma

Form-genus: **Crassipollis nov. f. gen.**

Derivatio nominis: after the thick nexine.

Genotype: *Crassipollis pusztavamensis* n. f. sp.

Generic diagnosis: Pollen grain of irregularly circular or oval contour as viewed in the E-plane, dorsoventrally flattened, mostly small and medium size rarely large, monosulcate, having a tectate — perforate sexine thinner than the nexine. P : e ratio: 2.5 to 1.7. Sexine clavate. Columella 0.3 to 3.8 μm high, composed of baculae of definite arrangement, the tectum being formed as a result of the fusion of the heads of these and pierced by fine tubuli.

The sulcus on the proximal side extends from pole to pole, being often widened along one of its ends, forming, as a rule, a thin split in the thin sexine and a radially dissected dissolving field in the thick nexine and dividing the grain into two more or less equal and symmetrical halves.

Differential diagnosis: With its thick exine, the thick sexine-nexine thickness ratio, the peculiar sulcus and the tectum structure, *Crassipollis* nov. form-genus distinctly deviates both from the hitherto-known tectate monosulcate pollen genera and from the ones here described. These features distinguish it from thin-walled *Clavatipollenites* Couper 1958, the similar *Rossipollis* W. Krutzsch 1970, the closely related *Retimonocolpites* Pierce 1961 and *Similipollis* nov. form-genera.

Remarks: Information sufficient for reconstruction of the exine structure of *Crassipollis* nov. f. gen. could only be obtained by a combined use of light microscope techniques with an aperture of 100/1.40 of the oil-immersion objective and SEM and TEM images of a magnification of $\times 10\,000$ and $\times 30\,000$, respectively Accordingly, the bacula forming the columella layer on the nexine are located concentrically by groups of 4 to 5 in such a form that they form at the same time one of the members of the adjacent circles as well. Formed of bacula the circles are arranged in more or less regular rows (lines) on the nexine. The hemispherical heads sitting at the tips of the baculae are intergrown along their E-plane and form a free tubulus reaching up to the nexine in the centre of the circles, thus resulting in a perforate tectum. The height of the bacula of the circle-forming clavae, their spacing and the size of the heads sitting at their tips are responsible, all combined, for the more or less fine or more or less coarse perforation characteristic of the individual *Crassipollis* species. As a result of the variance of these structural elements there is an ample spectrum of variation from an almost imperforate tectum, through a negative reticulum (when the lumen and the intermediate surface are more or less equal in size) up to a semitectate sexine which, when viewed from atop, appears to be perfectly reticulate (when the lumen is larger than the intermediate surface).

As observed by the authors, the *Crassipollis* species traceable from the Lower Albian up to the Lower Cenomanian show this trend of development of their sexine structure. The tectum of the older species is more compact, with a perforation of smaller lumen, than it is the case with the younger forms in which the sexine, when seen in top view, appears to be almost semitectate–microreticulate.

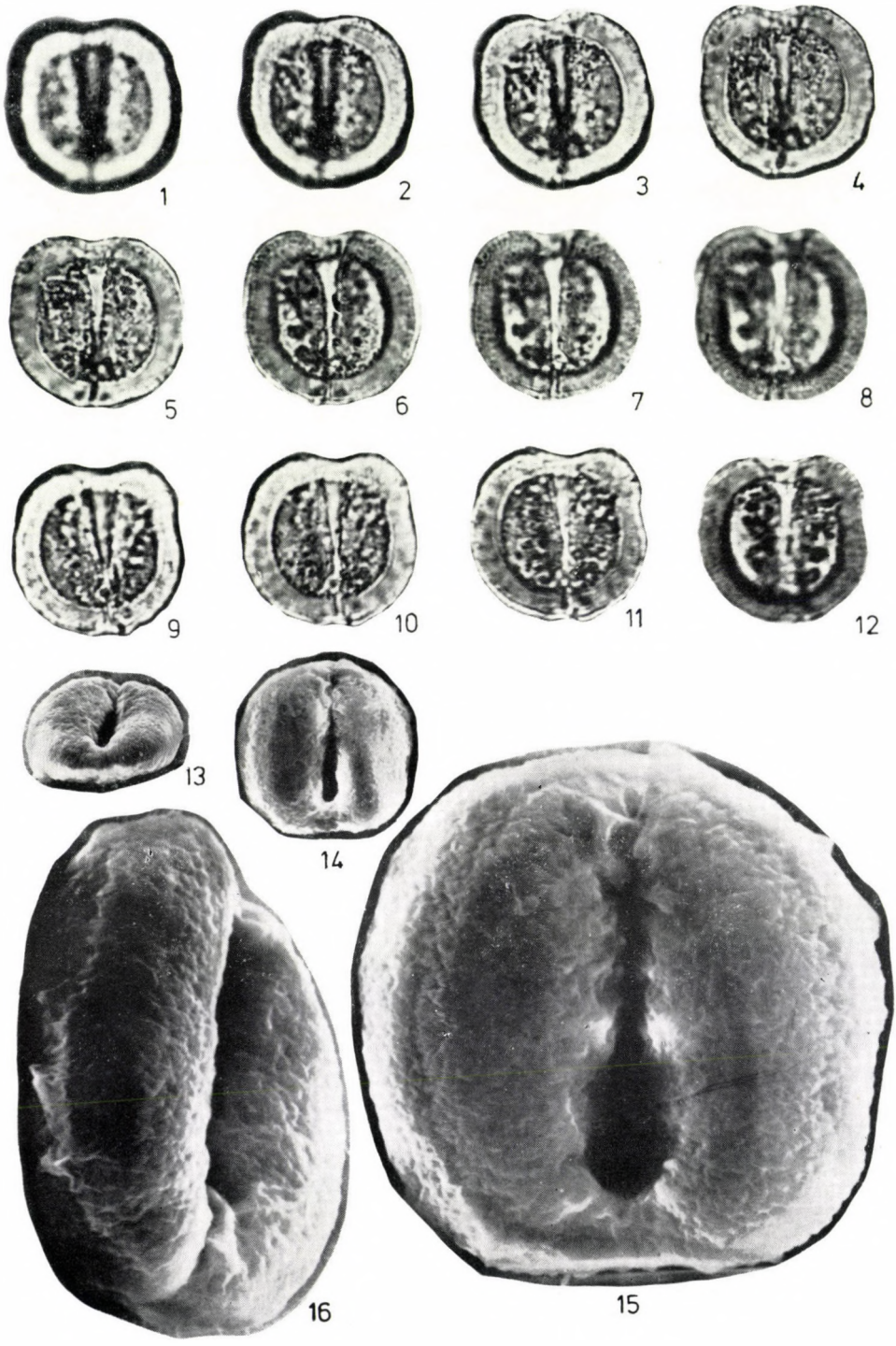
Crassipollis pusztavamensis nov. f. sp.

Plate I, Figs 1–16
Plate II, Figs 1–3

Derivatio nominis: after the locus typicus.
Locus typicus: borehole Pvt.-2 at Pusztavám.
Stratum typicum: dark grey argillaceous marl, Tés Clay Formation, Middle Albian, penetrated in the interval of 120.0 to 121.20 m.
Holotype: slide No. 18, specimen shown in Plates I–II.

Diagnosis: Prolate, spheroidal, thick-exined, tectate to perforate, monosulcate pollen grain, quadratic in shape, of medium size, with angles usually rounded in the E-plane and with slightly convex sides.

In longitudinal section the sulcus extends from wall to wall. In the thin sexine there is a thin split growing wider at one tip. In the thick nexine there is a radially irregularly dissected dissolving field along which the sexine is bent deep into the centre of the grain.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Nexine 3 to 4 μm thick, smooth, granulate in the dissolving field of the sulcus. Its inner surface is normally covered by a smooth lamella of 0.3 to 0.5 μm thickness.

Sexine 0.8 to 0.6 μm thick. Its columella layer is composed of rows of the 0.4 to 0.6 μm high bacula of the clavae that show a regular arrangement. The tectum is composed of a perforate layer resulting from the adhesion of the hemispherical heads 0.2 to 2.3 μm in diameter, of the clavae.

Size characteristics: largest diameter 24 to 26 μm, wall thickness 4 to 5 μm. Length of holotype 24 μm, its width 25 μm, its height approximately 8 μm, wall thickness 4 μm; *P/E* index: 0.9.

Description: based on SEM made from the distal surface of the type specimen: Originally roll-shaped, the grain is divided into two more or less equal and symmetrical, crescent-shaped halves (with the tips of the crescents grown together) by a deep furrow-like sulcus extending in the median of the body (Plate I, Figs 14–15).

Grouped circularly by fours or fives and adjusted to the pattern of the bacula of the columella, the intergrown heads of the clavae forming the tectum result in a shape resembling to the fructification of mallow or raspberry with a tubus, 0.2 μm, in the centre of each, piercing the sexine and widening in the shape of a funnel when reaching to the surface (Plate II, Fig. 2, a SEMG of 30 000 magnification of the type specimen).

These elements, when viewed from the sides, appear to be arranged in arched rows (lines) on the surface, having their convexity towards the sulcus (Plate II, Fig. 1, magnification ×10 000).

Differential diagnosis: *Crassipollis pusztavamensis* nov. form-species differs from ist closest relative, *Crassipollis urkutensis* nov. form-species, by its external contour and the finer structure of its tectum. The contour in the E-plane of *Crassipollis pusztavamensis* is a convexe-sided square with rounded angles, while that of *Crassipollis urkutensis* nov. f. sp. is circular.

The bacula forming the columella layer of *Crassipollis pusztavamensis* are densely packed, and the heads of the clavae are more concentrated than it is the case with *Crassipollis urkutensis* nov. sp. in which, because of the layer of less concentrated bacula, the heads are less concentrated too and thus they are reflected as a fine microreticulum at the surface (negative reticulum). *Crassipollis pusztavamensis* nov. gen. et sp. is different from *Crassipollis deakae* nov. f. sp., an otherwise also similar form, the difference consisting first of all in the size characteristics and the contour of the former. *Crassipollis deakae* nov. f. sp. is bigger (28–32 μm), thicker-walled (5.5–7.5 μm), *Crassipollis pusztavamensis* n. sp. being prolate, spheroidal, *Crassipollis deakae* nov. f. gen., in turn, is suboblate.

Remark: The first appearance of *Crassipollis pusztavamensis* nov. f. gen. et sp. corresponds to the lower part of the Middle Albian Tés Clay Formation, its last occurrence being in the lower, glauconitic reaches of the Pénzeskút Marl Formation—interval corresponding to the substuderi-Zone. Its acme falls in the upper third of the Tés Clay Formation.

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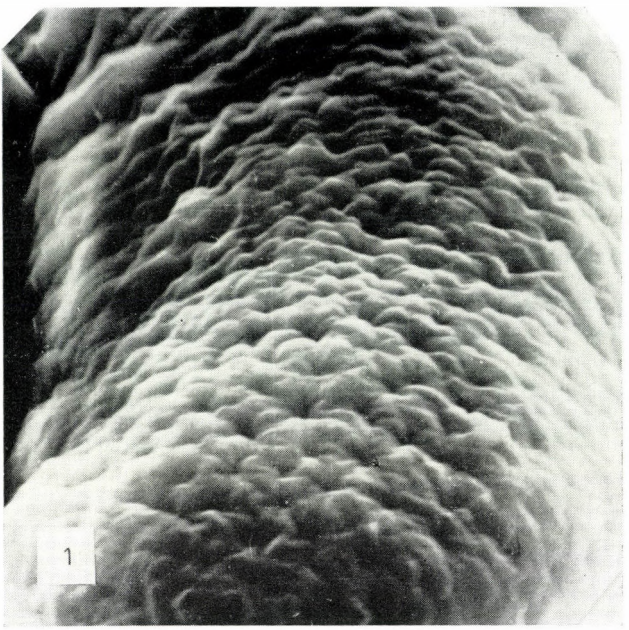
Plate I

Crassipollis pusztavamensis nov. f. gen. et sp. Pusztavám, borehole Pvt-2, 120.0–121.20 m; Tés Clay Formation, Middle Albian. 1–12. Light micrographs (Single grain preparation No 18, genotype). 1–8 = LO analysis of one side, 9–12 = LO analysis of the other side. 13–16. SEMG of the same grain. 13–14 = ×1000; 15 = ×3000; 16 = ×3000. The height of the grain can be readily measured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Crassipollis deakae nov. f. sp.

Plate IV, Figs 1–18

Synonym: *Corollaria annularis* Malj. in DEÁK 1953, p. 32–33, 65, Plate XII, Figs 12, 14.
Clavatipollenites deakae Góczán in NAGY 1971, p. 35 (nomen nudum).
Crassipollis deakae Juhász et Góczán 1976, p. 38, Plate I, Fig. 12 (nomen nudum).

Derivatio nominis: after the first describer of the species, geologist M. DEÁK.

Locus typicus: Pusztavám, borehole Ptv-2.

Stratum typicum: dark grey argillaceous marl intersected in the 120.0 to 121.20 m interval. Tés Clay Formation, Middle Albian.

Holotype: pollen grain, slide 13948/1, coordinates 14.3–107.5, Plate IV, Figs 1–18.

Diagnosis: Monosulcate, thick-exined pollen grain of medium size, slightly oval, suboblate and tectate-perforate, as viewed in the E-plane. Its polar axis is by 4 to 5 μm shorter than its equatorial diameter.

Sulcus extending from pole to pole along the longitudinal axis. In the sexine there is a simple split growing wider towards one of the poles. In the thick nexine, it passes over into a wide dissolving field which is radially dissected.

Exine about 5.0 to 7.5 μm thick. Sulcus becoming narrower at both ends, being a little bit depressed at one of them. Structurally, it is composed of a thin, structured sexine and a thick, smooth nexine. The inner surface of the nexine is covered by a smooth, 1 to 0.5 μm thick layer.

The nexine is about 4.3 to 5.8 μm thick, smooth over the larger part of the grain, but in the radially dissected dissolving field along the sulcus it is granulate, striate or verrucate.

The sexine is 1.2 to 1.6 μm thick, clavate. Its columella layer is constituted by dense rows of definitely arranged and 0.6 to 0.8 μm high bacula of the clavae. The tectum is a perforate layer resulting from the adhesion or fusion of the very fine heads, circa 0.5 μm in diameter and 0.6 to 0.8 μm high. The perforation is represented by tubules with a lumen of 0.1 to 0.2 μm width, spaced at about 0.5 μm intervals, thus piercing the sexine.

Size range: The largest diameter varies between 26 and 36 μm, wall thickness 5 to 7 μm. Length of holotype 26 μm, width 31 μm, height 8 μm, wall thickness: along the poles 4 μm, in the E-axis: 7 μm, $P/E = 0.8 : 1$.

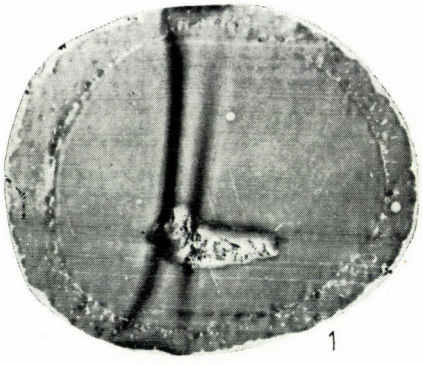
Differential diagnosis: With its shape, size and the pattern of the nexine, *Crassipollis deakae* nov. f. sp. differs quite clearly from all representatives of *Crassipollis* f. sp.

Remark: On the type specimen the compact nexine is broken as a result of the strong compression that has hit the grain. The tectate-perforate and thin sexine, however, is not, but, dissociated from the broken nexine, it has been flexibly depressed following the direction of fracture.

Crassipollis deakae n. f. sp. appears in the Tés Clay Formation/Middle Albian/and ist last representatives are traceable in the dispar-Zone of the Upper Vraconian substage.

Plate II

Crassipollis pusztavamensis nov. gen. et sp. SEMGs of the genotype. 1. SEMG taken of the specimen from the sulcus up to the margin of the flank in the E-plane. Note the pattern of resembling to the fructification of mallow forming the tectum. Note also their surface arrangement and the funnel-shaped openings of the perforation between them. Magnification $\times 10\,000$. 2. SEMG of magnification of $\times 30\,000$. Detail from the former stretch of shell. 3. SEMG of magnification of $\times 30\,000$. Detail from the narrower end of the sulcus



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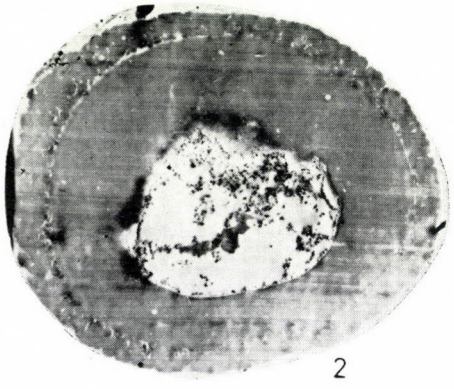

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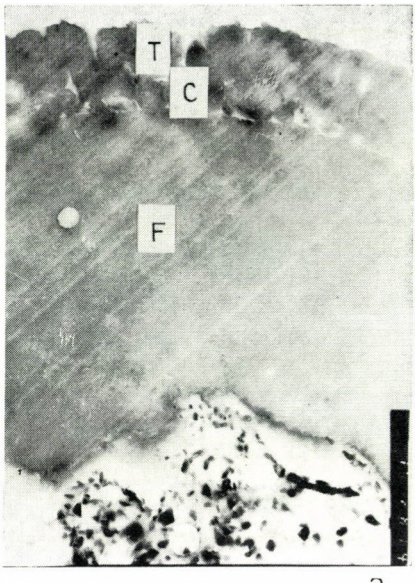

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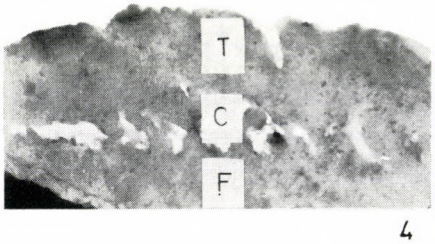

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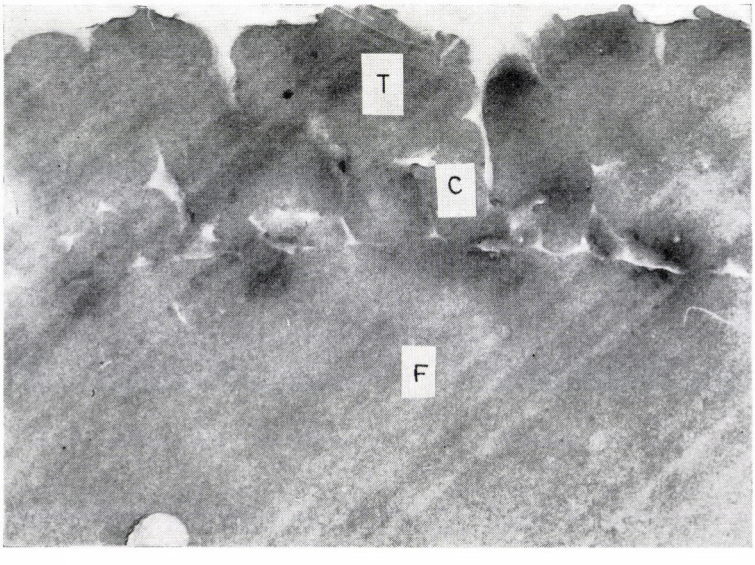

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Crassipollis dissimilis nov. f. sp.
Plate VII, Figs 1–12

Synonym: *Crassipollis dissimilis* Juhász et Góczán 1976, p. 38, Plate I: 11 (nomen nudum).

Derivatio nominis: dissimilis (l) = dissimilar, different. The denomination is based on the fact that the species being described is different from the other representatives of *Crassipollis* f. sp.

Locus typicus: Hárskút, borehole Hk-4.

Stratum typicum: 204.5 to 207.0 m, grey "Turrilites Marl", Pénzeskút Marl Formation, Upper Vraconian dispar-Zone.

Holotype: pollen grain, slide 467/3, coordinates 21.3–98.7, Plate VII, Figs 1–12.

Diagnosis: Monosulcate pollen grain, of medium size, prolate spheroidal, thick-exine, tectate-perforate, oval as viewed in the E-plane.

Sulcus along the polar axis extending from pole to pole. In the thin sexine there is a simple, narrow split. One of its tips grows wide at the pole. In the thick nexine it forms a radially-widening dissolving field.

Exine 3.5 to 4.5 μm thick, depressed along the sulcus and getting thinner. It is composed of a thicker inner layer and a thinner, structured outer one.

Nexine 2.3 to 2.8 μm thick, smooth, except for the dissolving field along the sulcus. Along the sulcus it is granulate. Its inner surface is covered by a lamella of 0.3 to 0.5 μm thickness.

Sexine 1.2 to 1.5 μm thick, tectate-perforate. Its columella layer is formed of 0.8 to 1.0 μm thick densely concentrated bacula of clavae. The perforate tectum consists of the merged heads of the clavae. Responsible for the perforation, the surface openings of the tubules are 0.2 to 0.3 μm in diameter.

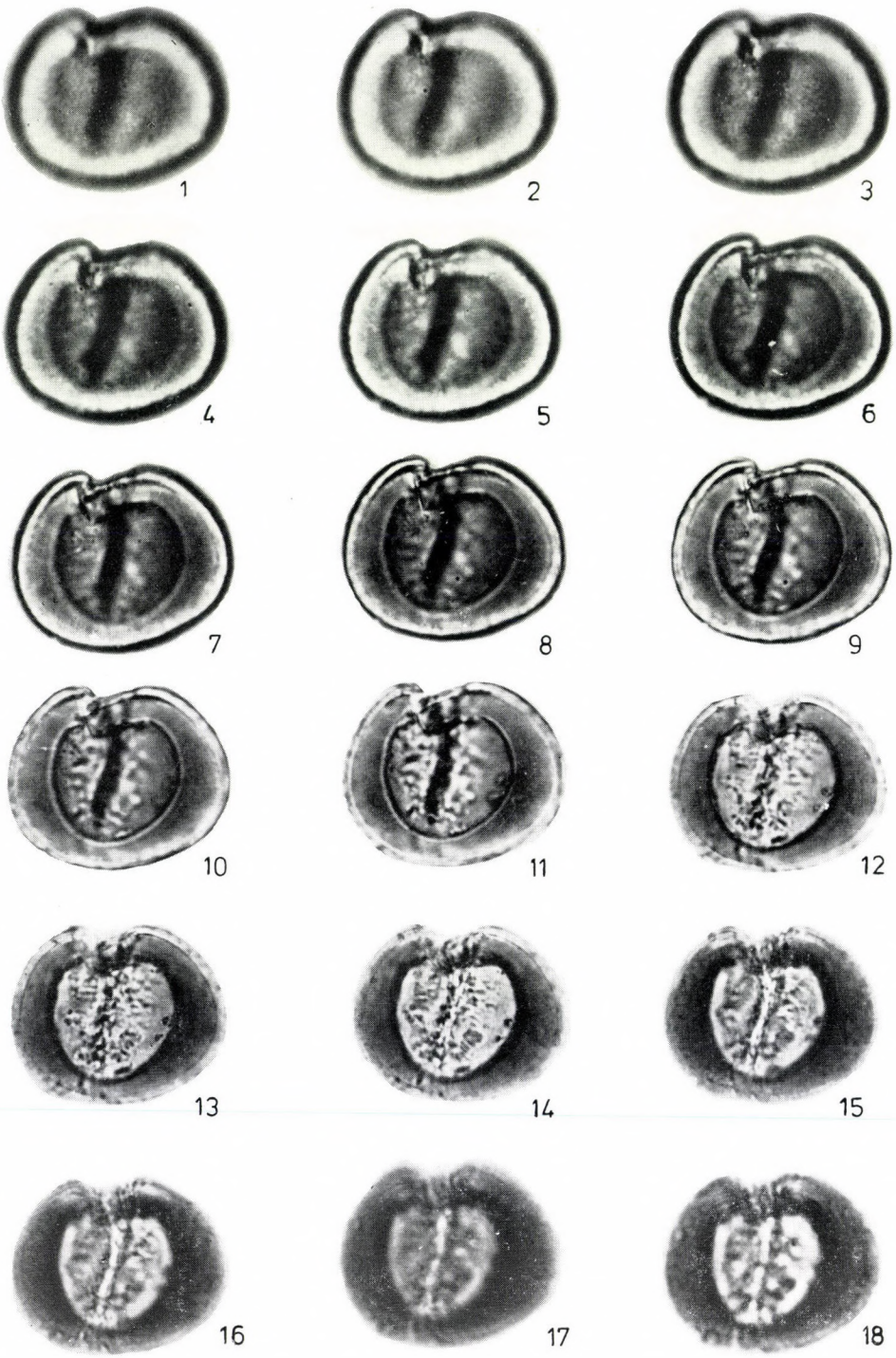
Size range: 22–26 μm $\times$ 22–25 μm, wall thickness 3.5–4.5 μm. Length of holotype 26 μm, its width 25 μm, its wall thickness 4.5 μm, its *P/E* index: 1.0.

Differential diagnosis: With its size characteristics and proportions, *Crassipollis dissimilis* nov. f. sp. shows the greatest resemblance to *Crassipollis ovalis* n. f. sp. However, with its external prolate spheroidal axis ratio, and its poles slightly depressed at their tips, it can be easily distinguished from *Crassipollis ovalis* n. f. sp. which is prolate, more elongated along the polar axis. From *Crassipollis pusztavamensis* n. f. sp., form similarly prolate spheroidal, but with angles rounded off, it deviates both by its outer contour and its thinner nexine.

Remark: Typical specimens of *Crassipollis dissimilis* nov. sp. have so far been encountered only in rocks belonging to the Upper Albian dispar-Zone of the Pénzeskút Marl Formation. A species of rare occurrence.

Plate III

Crassipollis sp. 1–3, 5. TEMGs from a drop slide. 1–2. Subequatorial sections, $\times$3300. In the lower part of 2 the sexine-nexine thickness can be measured. In 3 the columnar layer of the columella, the longitudinal section of elements resembling to the fructification of mallow or raspberry, the tubuli between them, piercing the sexine and extending up to the thick foot layer with their funnel-shaped outer openings, can be seen. 5. Detail of 3 (ca. $\times$28 148). 4. TEMG of another grain, $\times$10 000. Tangential section from the columnar layer of the columella (bacula) and the tectum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Crassipollis vraconicus nov. f. sp.

Plate V, Figs 1–22

Synonym: *Crassipollis tubulosus* Juhász et Góczán 1976, p. 38, Plate 1, Fig. 14 (nomen nudum).
Derivatio nominis: after its acme.
Locus typicus: Bakonynána, outcrop.
Stratum typicum: Bed II, grey Turrilites Marl, Pénzeskút Marl Formation, Upper Albian, Upper Vraconian, dispar-Zone.
Holotypus: specimen in slide II/1–3, coordinates 9.2–96.0, Plate V, Figs 1–9.

Diagnosis: Monosulcate pollen grain of irregularly circular or slightly ellipsoidal shape, of medium size, prolate spheroidal, tectate-perforate and thick-exined, as viewed in the E-plane. Its length of polar axis and equatorial diameter are equal or the E-axis is by 1 or 2 microns shorter.

Sulcus along the longitudinal axis extending from pole to pole. In the thin sexine there is a simple split, in the thick nexine it passes over into a dissolving field that widens in radial direction.

Exine 5 to 6 μm thick, tectate-perforate. Nexine 3 to 4 μm thick. Over its larger part the grain is smooth, being granulate in the 8 to 10 μm wide dissolving field formed along the sulcus. Its inner surface is covered by a smooth lamella circa 0.5 μm thick.

The sexine is clavate, 1.5 to 2.0 μm thick, its columella layer consists of the bacula of the clavae. The tectum is composed of a perforated layer resulting from the coalescence of the heads of the claves. The diameter of the opening of the perforation as exposed to the surface is 0.5 to 08. μm, being nearly equal to, or sometimes greater than, the diameter of the coalesced heads of the clavae. The tectum and the columella are more or less equally thick. So the structure appears to be microfoveolate or microreticulated as reflected at the surface.

Size range: Largest diameter between 27 and 32 μm, wall thickness between 5 and 6 μm. Length of holotype circa 32 μm, its width 31 μm, its wall thickness 6 μm, $P/E = 1 : 1$.

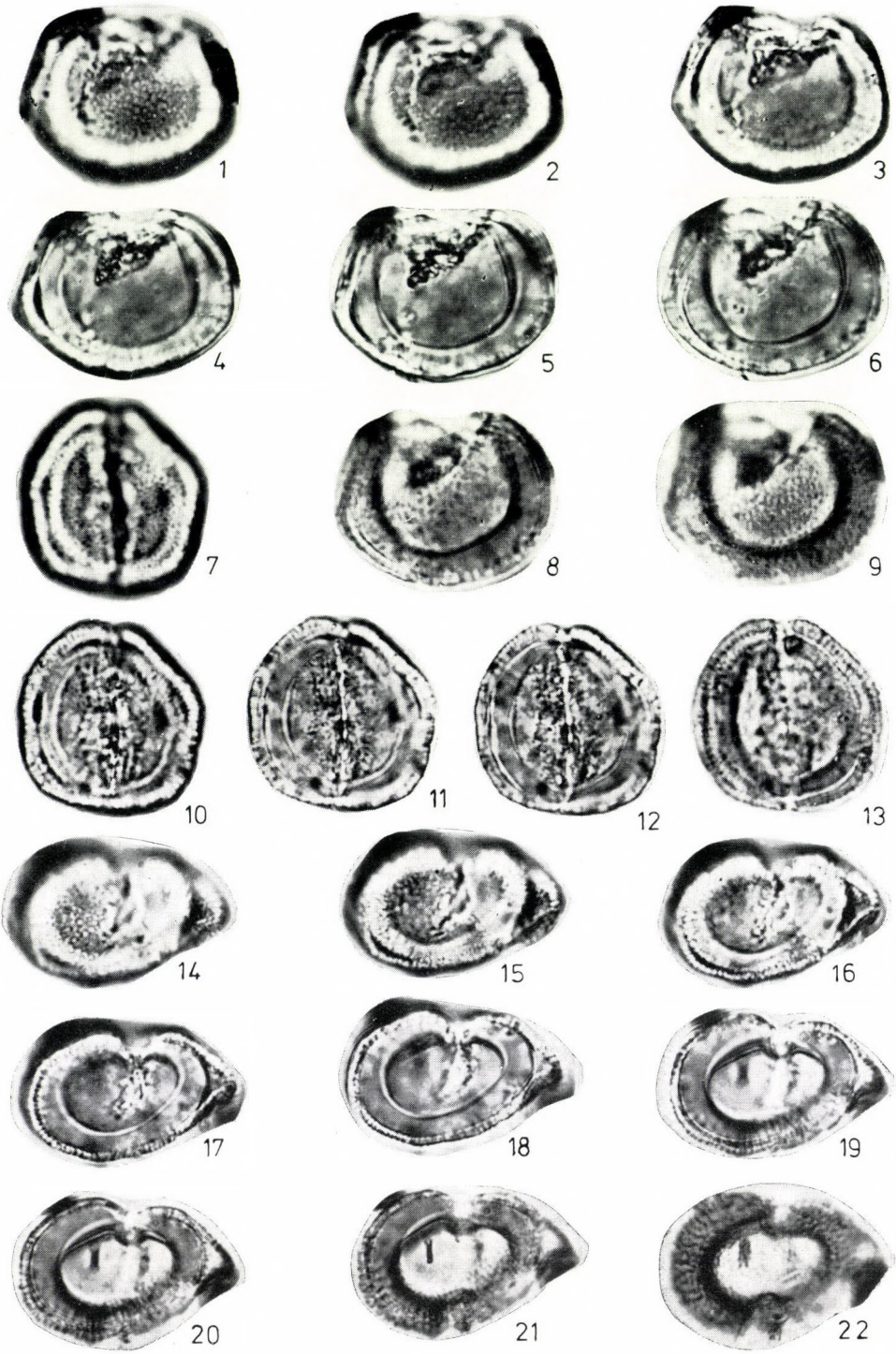
Differential diagnosis: It is by the coarser perforation of the sexine, the greater size of the openings and the greater spacing of the columella-forming bacula that *Crassipollis vraconicus* n. f. sp. differs from the other *Crassipollis* n. form-species of similar size and contour and from *Crassipollis deakae* n. f. sp. of similar wall thickness.

Remark: Relatively high and, compared to the form-species so far discussed, of greater spacing of circular rows, the bacula assures already a more loose connection with the sexine. For this reason, upon mechanical impact, the sexine is often flexibly disintegrated from the nexine, resulting in a partial or complete interloculum.

The first specimens of *Crassipollis vraconicus* nov. f. sp. were found in the "glauconitic marls" of the Pénzeskút Marl Formation—marls belonging to the Lower Vraconian substuderi-Zone, and have so far never been encountered in rocks younger than the Upper Vraconian dispar-Zone.

Plate IV

1–18. *Crassipollis deakae* nov. sp. Light micrographs of holotype, ×1000. Pusztavám, borehole Pvt-2, 120.0–121.20 m; Munieria Clay Marl facies, Tés Clay Formation, Middle Albian. Grain in slide 13948/1, coordinates 14.3–107.5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Crassipollis ovalis nov. f. sp.
Plate VI, Figs 1–20

Derivatio nominis: after its E-contour.

Locus typicus: Csehbánya, borehole Cs-5.

Stratum typicum: 262.0–263.0 m, dark grey argillaceous marl, Tés Clay Formation, Middle Albian.

Holotype: grain in slide II/a-2, coordinates 17.6–96.6, Plate VI, Figs 1–6.

Diagnosis: Monosulcate pollen grain, ellipsoidal in shape, when viewed in the E-plane, of medium size, prolate, thick-exined, tectate-perforate, with a longitudinal axis by 1 to 3 microns larger than the E-axis.

The sulcus in the thin sexine is a narrow simple split extending from pole to pole along the polar axis; in the thick nexine it often passes over into a wider, granulate-verrucate dissolving field.

Exine, along the E-axis, 4 to 5 μm thick, along the sulcus, a little bit thinner. Structurally, it is composed of a thicker, structureless nexine and of a thinner, clavate sexine.

Nexine 3 to 4 μm thick, smooth over the larger part of the grain, being granulate-verrucate in the dissolving field along the sulcus.

Sexine about 1 μm thick, tectate-perforate. The columella layer is formed by the closely-packed, regular and dense rows of the bacula of the clavae. The tectum is a perforated layer consisting of the merging heads of the clavae. The diameter of the outer opening of the tubuli is 0.2 to 0.3 μm.

Size range: Length 27 to 28 μm, width between 24 and 26 μm, wall thickness between 4 and 5 μm. Size of the holotype 28×24 μm, its wall thickness 4 μm, $P/E = 1.2 : 1$.

Differential diagnosis: By its oval shape, consistently elongate along the longitudinal axis, *Crassipollis ovalis* n. f. sp. is readily distinguished from *Crassipollis urkutensis* nov. f. sp. of similar size but suboblate. Because of its larger size and coarser perforation, it differs from *Crassipollis vertesensis* nov. f. sp., species otherwise most closely related to it.

Crassipollis vertesensis nov. f. sp.
Plate VII, Figs 13–27

Derivatio nominis: after the area of distribution (Vértes Mountains) of the type.

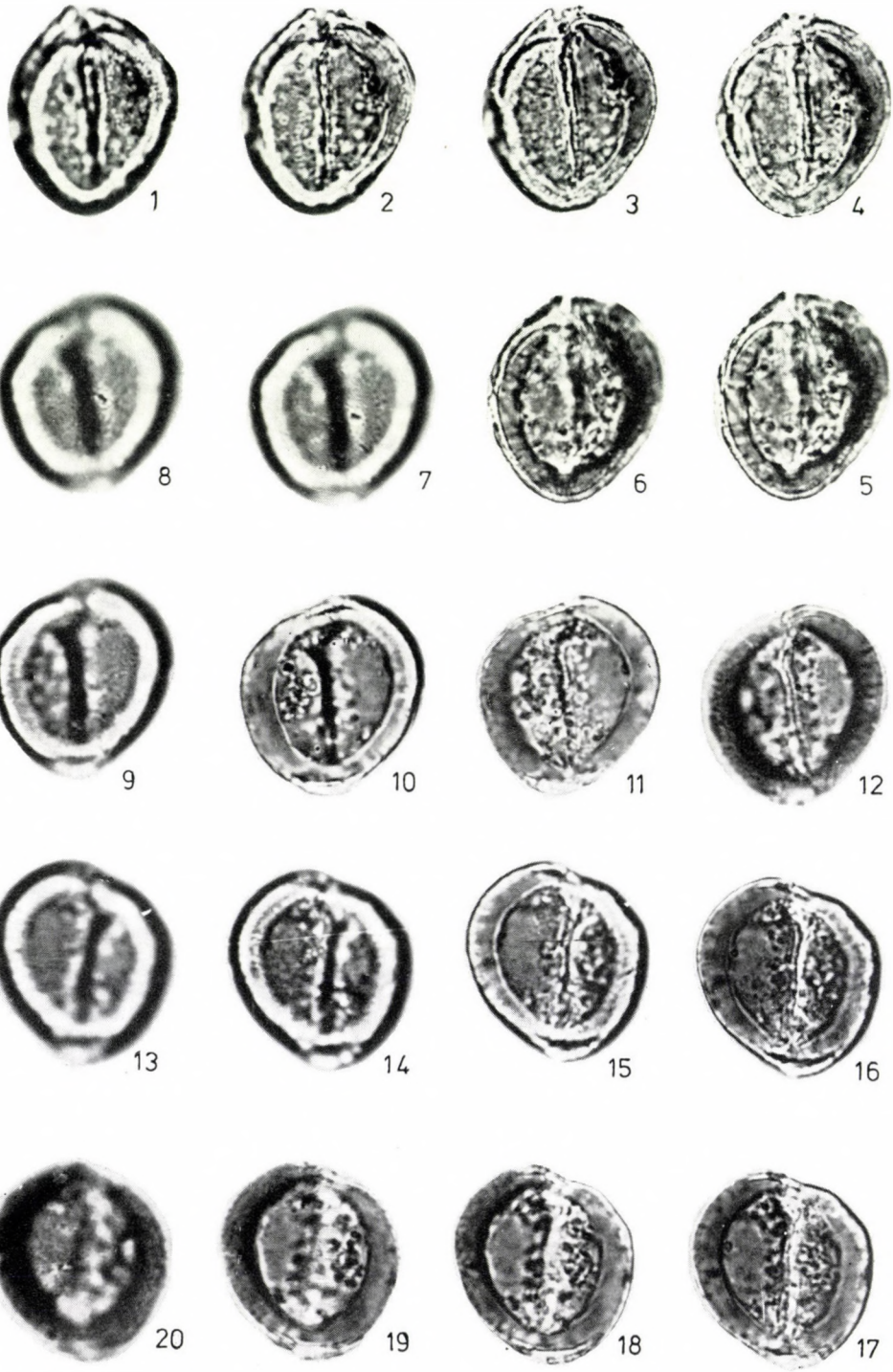
Locus typicus: Vértessomló, borehole Vst-5.

Stratum typicum: 58.5–61.5 m, dark grey siltstone, Vértessomló Siltstone Formation, Lower Albian, mamillatum-Zone.

Holotype: grain in slide 58–61.5/1, coordinates 6.0–100.1, Plate VII, Fig. 13–19.

Plate V

1–9. *Crassipollis vraconicus* nov. sp. (holotype). Bakonynána outcrop, Bed II/1–3. Pénzeskút Siltstone Formation, Upper Vraconian, dispar-Zone, bergeri-Subzone. Grain in slide II/1–3, coordinates 9.2–96.0. Light micrographs of holotype, $\times 1000$. 10–13. *Crassipollis vraconicus* nov. sp. (paratype). Pusztavám, borehole Pvt-2, 87.5 m, glauconitic marl facies, Pénzeskút Siltstone Formation, Upper Albian, Lower Vraconian, blancheti-Subzone. Grain in slide 13939/1, coordinates 45.7–117.4. Light micrographs of paratype, $\times 1000$. 14–22. *Crassipollis vraconicus* nov. sp. (paratype) Bakonynána outcrop, Bed 2/1. Pénzeskút Silstone Formation, Upper Albian, Upper Vraconian, dispar-Zone, bergeri-Subzone. Grain in slide II-2, coordinates 17.8–98.5. Light micrographs of paratype, $\times 1000$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Diagnosis: Monosulcate pollen grain of ellipsoidal shape, as viewed in the E-plane, of medium size, prolate, of a thick exine, tectate-perforate, with a polar axis by 3 to 5 μm longer than the E-axis.

The sulcus along the longitudinal axis extends from pole to pole. In the sexine it forms a simple, narrow split, in the nexine a granulate dissolving field. Exine 2.5 to 3.0 μm thick. It consists of an inner, thicker, structureless (nexine) and an outer, thinner and tectate-perforate layer (sexine).

The nexine is by about 2× thicker than the sexine: 1.6 to 2.0 μm. At its larger part of the grain is smooth, in the dissolving field of the sulcus it is granulate.

The sexine is tectate-perforate or clavate, 0.8 to 1.0 μm thick and both ends of the sulcus often dissociate from the sexine, thus resulting in an interloculum.

The columella consists of the bacula of the clavae. The bacula are 0.5 to 0.6 μm high and closely packed. The tectum is composed of a perforated layer produced by the fusion of the heads of the clavae. The perforation is extremely fine, the surface openings of the tubuli are circa 0.1 to 0.2 μm wide.

Size range: Length circa 24 μm, width 19 to 20 μm, wall thickness circa 2.5 to 3 μm. Size of holotype 24×20 μm, wall thickness 3 μm, $P/E = 1.2 : 1$.

Differential diagnosis: *Crassipollis vertesensis* n. f. sp. resembles most to *Crassipollis ovalis* n. f. sp. from which it deviates with its smaller size characteristics (size, wall thickness) and more slender shape.

Remark: Built up of densely-packed rows of bacula, the columella layer of *Crassipollis vertesensis* n. f. sp. is often observed to be separated, together with the very finely perforated tectum, from the nexine along both ends of the sulcus and to form an interloculum.

Crassipollis minor nov. f. sp.

Plate VIII, Figs 1–39

Synonym: *Crassipollis minor* Juhász et Góczán 1976, p. 38, Plate 1: 8 (nomen nudum).

Derivatio nominis: after its size.

Locus typicus: Hárskút, borehole Hk-4.

Stratum typicum: 124.7 to 127.8 m, grey Turrilites Marl, Pénzeskút Marl Formation, Upper Vraconian, dispar-Zone.

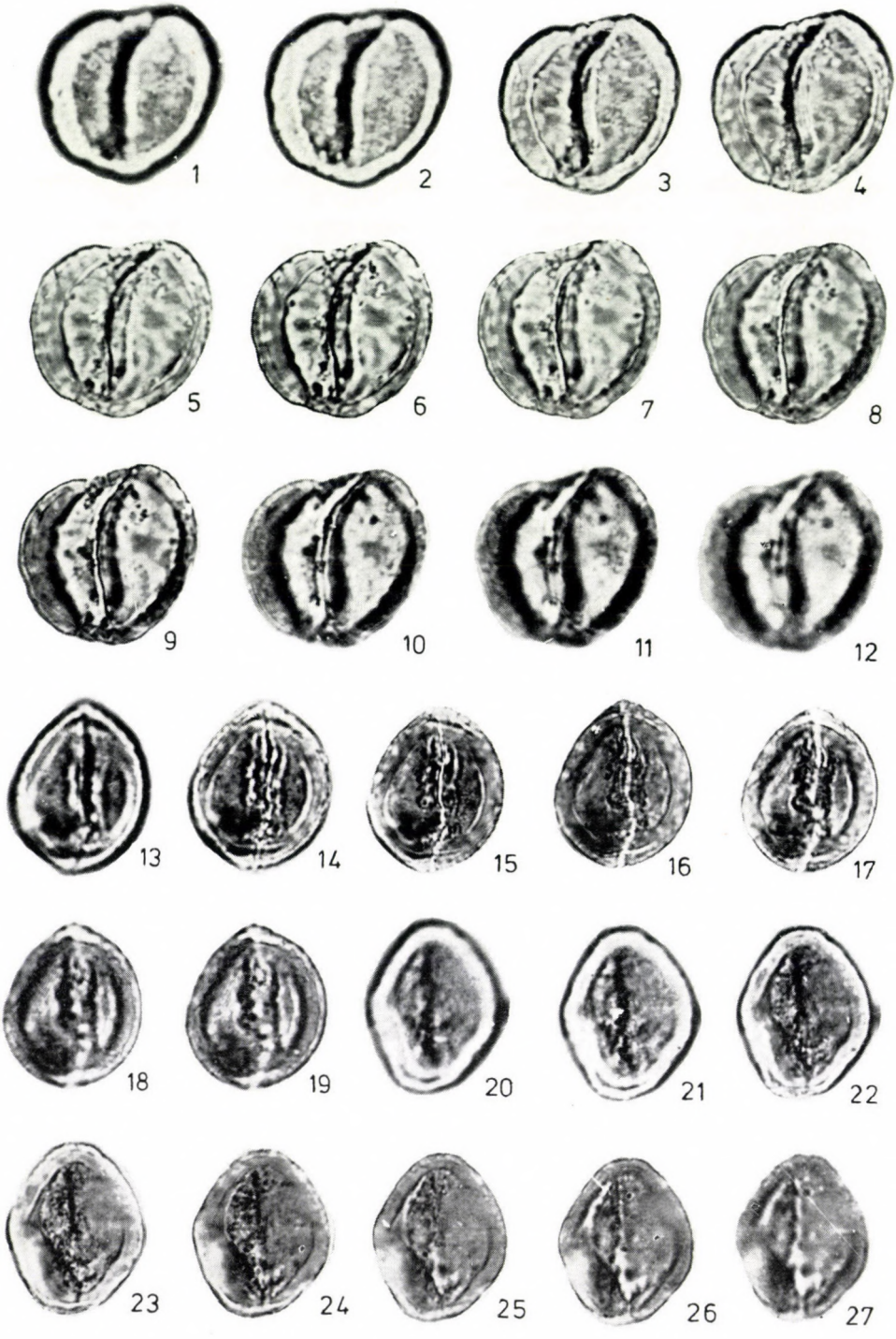
Holotype: specimen in slide 14/I, coordinates 18.9–115.4, Plate VIII, Fig. 1–13.

Diagnosis: Monosulcate pollen grain of circular or slightly oval shape, when viewed in the E-plane, of small size, oblate spheroidal, thick-exined and tectate-perforate having a polar axis often by 1 to 2 microns shorter than the equatorial diameter, or, less frequently, nearly equal to it.

The sulcus along the polar axis reached from pole to pole, being represented, in the thin sexine, by a more or less straight, narrow split which depressed, like a furrow, into the thick nexine, is converted into a wider, disproportionately dissected dissolving field.

Plate VI

1–6. *Crassipollis ovalis* nov. sp. (holotype) Csehbánya, borehole Cs-5, 262.0–263.0 m, Munieria Clay-Marl facies, Tés Clay Formation, Middle Albian. Grain in slide II/6–2, coordinates 17.6–96.6. Light micrographs of holotype, ×1000. 7–12. *Crassipollis ovalis* nov. sp. (paratype) Pusztavám, borehole Pvt-2, 120.0–121.20 m, Munieria Clay-Marl facies, Tés Clay Formation, Middle Albian. Single grain slide. Light micrographs, ×1000. 15–20. The same grain as photographed from the other side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Exine 3 to 4 μ thick, becoming thinner along the sulcus and often slightly flattened at the two poles. It is composed of an inner, thick and structureless (nexine) and an outer, thin and structured layer (sexine).

The nexine is 2.3 to 3.0 μm thick, smooth at the larger part of the grain and granulate in the tapering dissolving field of the sulcus.

Sexine 0.7 to 1.0 μm thick. The columella layer is constituted by densely-packed and regular rows of bacula of about 0.4 to 0.6 μm height. The tectum consists of a perforated layer resulting from the adhesion of the hemispherical heads sitting at the tips of the bacula. At their opening to the surface, the perforations have a diameter of circa 0.1 to 0.2 μm.

Size range: Length 18 to 20 μm, width 18 to 21 μm, wall thickness between 3 and 4 μm. Length of holotype 19 μm, its width 20 μm, its wall thickness 3 μm, $P/E = 0.9$.

Differential diagnosis: Given its size and proportions (largest diameter versus wall thickness, sexine versus nexine), *Crassipollis minor* nov. f. sp. is easy to distinguish from all *Crassipollis* f. sp. of medium and low size.

Remark: The first representatives of *Crassipollis minor* nov. f. sp. appear in the mamillatum-Zone of the Vértessomló Siltstone Formation, i.e. in the lower reaches of the Albian and can be traced up to the formations belonging to the Lower Cenomanian mantelli-Zone of the Pénzeskút Marl Formation. The acme of the species in question is in the dispar-Zone. It is of longest stratigraphic range of all the *Crassipollis* species.

Subturma: Tenuinexines **nov. subturma**

Infraturma: *Tenuinexines – Nonreticulati* **nov. infraturma**

Subinfraturma: Tenuinexines–Nonreticulomonosulcati **nov. subinfraturma**

Form-genus: **Transitoripollis nov. f. gen.**

Derivatio nominis: transitus = latin for transitional. Reference to the presence of a transition between Gymnospermae and Angiospermae.

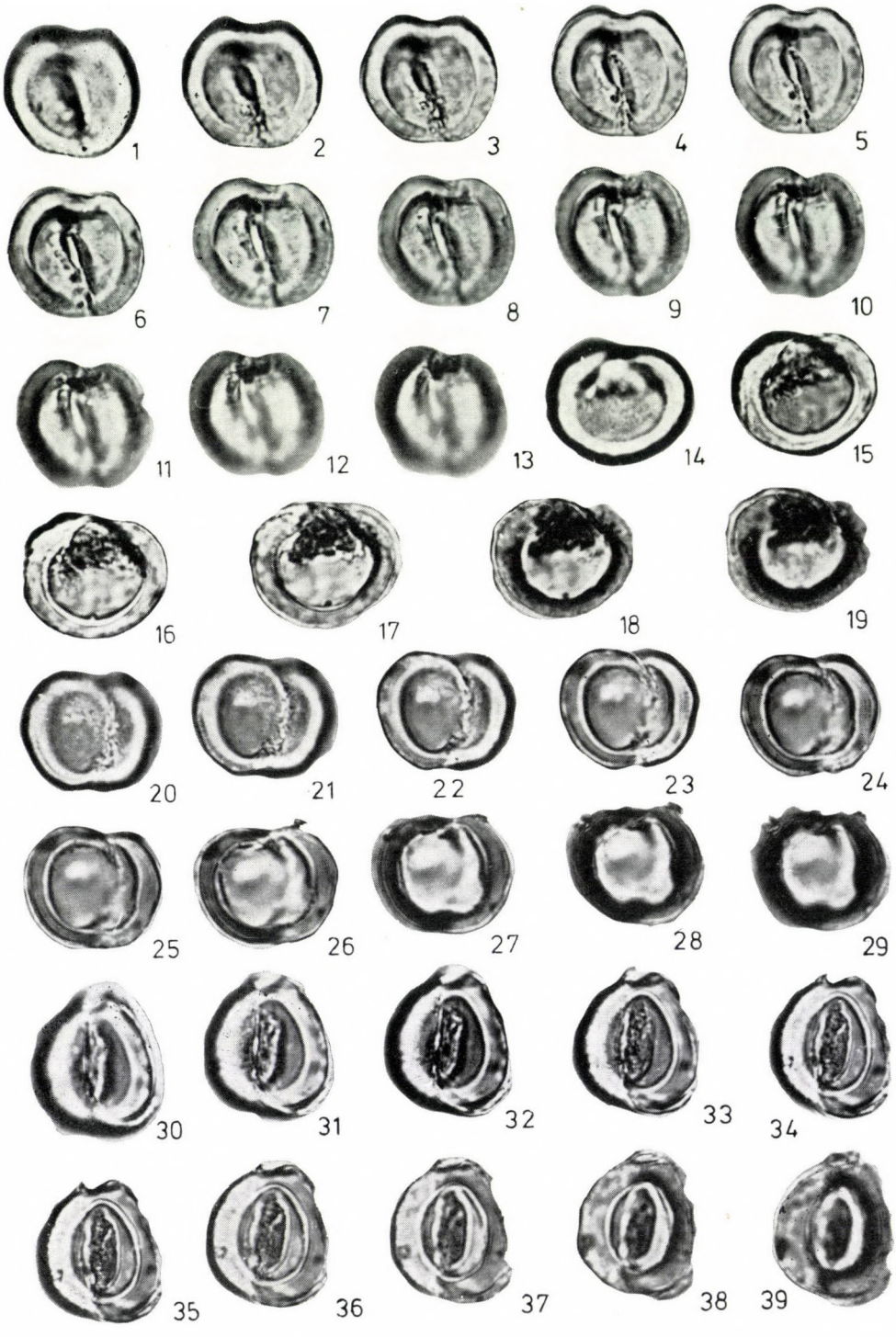
Genotype: *Transitoripollis anulisulcatus* nov. f. gen. et f. sp.

Generic diagnosis: Small, thin-exined, tectate-perforate monosulcate pollen grain, circular or ellipsoidal in shape when viewed in the E-plane, dorsoventrally slightly depressed with a sexine more or less equal in thickness with the nexine.

Its sulcus runs parallel to the longitudinal axis, but is shorter than that; the simple split opening equally in both the sexine and the nexine is seldom closed, being for the most part widely open. The exine is thinner than 2 μm, consisting of an unsculptured, smooth nexine and a sculptured sexine.

Plate VII

1–12. *Crassipollis dissimilis* nov. sp. (holotype) Hárskút, borehole Hk-4, 204.5–207.0 m, Turrilites Marl facies, Pénzeskút Siltstone Formation, Upper Vraconian, dispar-Zone, bergeri-Subzone. Grain in slide 467/3, coordinates 21.3–98.7. Light micrographs of holotype, ×1000.
13–19. *Crassipollis vertesensis* nov. sp. (holotype) Vértessomló, borehole Vst-5, 58.5–61.5 m, grey siltstone facies, Vértessomló Siltstone Formation, Lower Albian, mamillatum-Zone. Grain in slide 58.5–61.5, coordinates 6.0–100.1. Light micrographs of holotype, ×1000.
20–27. *Crassipollis vertesensis* nov. sp. (paratype) Vértessomló, borehole Vts-4, 181.0 m, grey siltstone facies. Vértessomló Siltstone Formation, Lower Albian, mamillatum-Zone. Grain in slide 181/1, coordinates 10.1–101.0. Light micrographs of paratype, ×1000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The sexine is usually as thick as the nexine. When viewed with an light microscope equipped with and objective of an aperture of 100/1.40, it appears to be chagrenate, with SEM shows in turn a microverrucate sculpture. The verrucae occur in ones or twos, less frequently in threes, 0.1 to 0.2 μm in size, intergrown along their base, covering the surface uniformly densely. They are often arranged in a form similar to the case of *Crassipollis*.

Differential diagnosis: With its small size, its tectate sexine and the peculiar features of its sulcus, *Transitoripollis* nov. f. gen. can be readily distinguished both from the hitherto-known pollen genera and from the monosulcate pollen genera now being described, deriving from angiospermous plants.

On the basis of its light microscopic image it resembles most to the Mezosoic, monosulcate pollen genera related to *Cycas* and *Ginkgo* as well as to the small-sized species of the genus *Crassipollis* n. f. gen. here described from which, however, it sharply deviates with its peculiar sulcus, its verrucate ultrasculpture and its *P/e* ratio.

Remark: The first representatives of *Transitoripollis* nov. f. gen. appear in the Lower Albian tardefurcata Zone, in the Vértessomló Siltstone Formation, its last individuals being encountered in the Middle Albian Tés Clay Formation. Its acme corresponds to the middle part of the Middle Albian.

Transitoripollis anulisulcatus nov. f. sp.

Plate IX, Figs 1–14 and 44–51

Synonym: *Transitoripollis anulisulcatus* Juhász et Góczán 1976, p. 38, Plate I: 1 (nomen nudum).

Derivatio nominis: annulus = latin for ring, after the ring-shaped sulcus.

Locus typicus: Oroszlány, borehole O–1825.

Stratum typicum: 529.1–530.2 m, dark grey argillaceous marl, Tés Clay Formation, Middle Albian.

Holotype: grain in slide No. 2, coordinates 6.4–108.7, Plate IX, Figs 44–51.

Diagnosis: Small-sized, oblate spheroidal, thin-exined, tectate-perforate, monosulcate pollen grain of circular or slightly oval shape in the E-plane.

The sulcus extends in the longitudinal axis, is usually shorter than this, often widely open, breaking through both layers of the exine.

The exine is 1.2 to 2.0 μm thick, consisting of an inner, unsculptured and an outer sculptured layer. The sexine and the nexine are almost equally thick.

The nexine is 0.6 to 1.0 μm thick, smooth, sculptureless, tightly adhering to the sexine, with no dissolving field along the sulcus.

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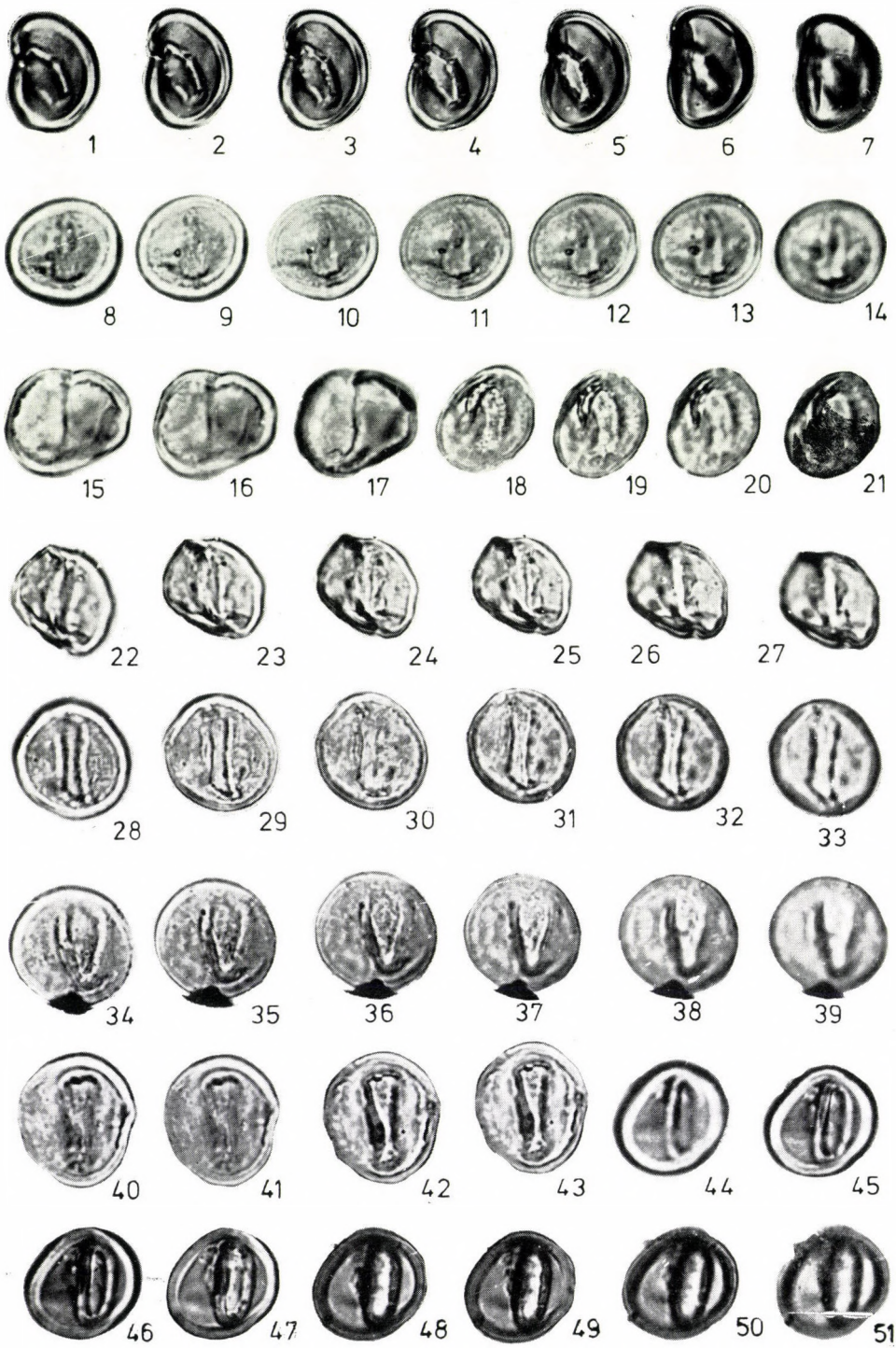
Plate VIII

1–13. *Crassipollis minor* nov. sp. (holotype). Hárskút, borehole Hk-4, 124.7–127.9 m, Turrilites Marl facies, Pénzeskút Siltstone Formation, Upper Vraconian, dispar-Zone, bergeri-Subzone. Grain in slide 14/1, coordinates 18.9–115.4. Light micrographs of holotype, ×1000. 14–19. *Crassipollis minor* nov. sp. (paratype). Hárskút, borehole Hk-4, 127.9–130.6 m, Turrilites Marl facies, Pénzeskút Siltstone Formation, Upper Vraconian, dispar-Zone, bergeri-Subzone. Grain in slide 45/3, coordinates 18.5–11.4. Light micrograph of paratype, ×1000. 20–23. *Crassipollis minor* nov. sp. (paratype). Csehbánya, borehole Cs-5, 225.5–226.0 m, Requienia-Orbitolina Limestone facies, an intercalation, Zirc Formation, lower part of the Upper Albian, inflatum-Zone. Grain in slide 7/3, coordinates 8.3–107.1. Light micrographs of paratype, ×1000. 30–39. *Crassipollis minor* nov. sp. (paratype). Hárskút, borehole Hk-4, 124.7–127.9 m, Turrilites Marl facies, Pénzeskút Siltstone Formation, Upper Vraconian, dispar-Zone, bergeri-Subzone. Light micrographs of paratype, ×1000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The sexine is 0.5 to 1.0 μm thick, tightly adhering to the nexine, chagrenate when viewed under the optical microscope, of a microverrucate ultrasculpture when examined by SEM and of a perforate structure when studied by TEM.

Size range: Length between 15 and 18 μm, wall thickness circa 1.8 μm, *P/E*: 1, *P/e* = 8.8.

Differential diagnosis: With its size, wall thickness, shape and anular sulcus, *Transitoripollis anulisulcatus* nov. f. gen. et f. sp. dissociates very well from *Transitoripollis similis* nov. f. sp. standing closest to it, but having a more circular shape, thinner wall and narrower sulcus.

Remark: Thus far *Transitoripollis anulisulcatus* nov. f. sp. has been recovered from the Middle Albian beds of the Tés Clay Formation only. It is one of the most frequent monosulcate pollen grains in this formation. It occurs throughout the area of distribution of the formation.

Transitoripollis similis nov. f. sp.

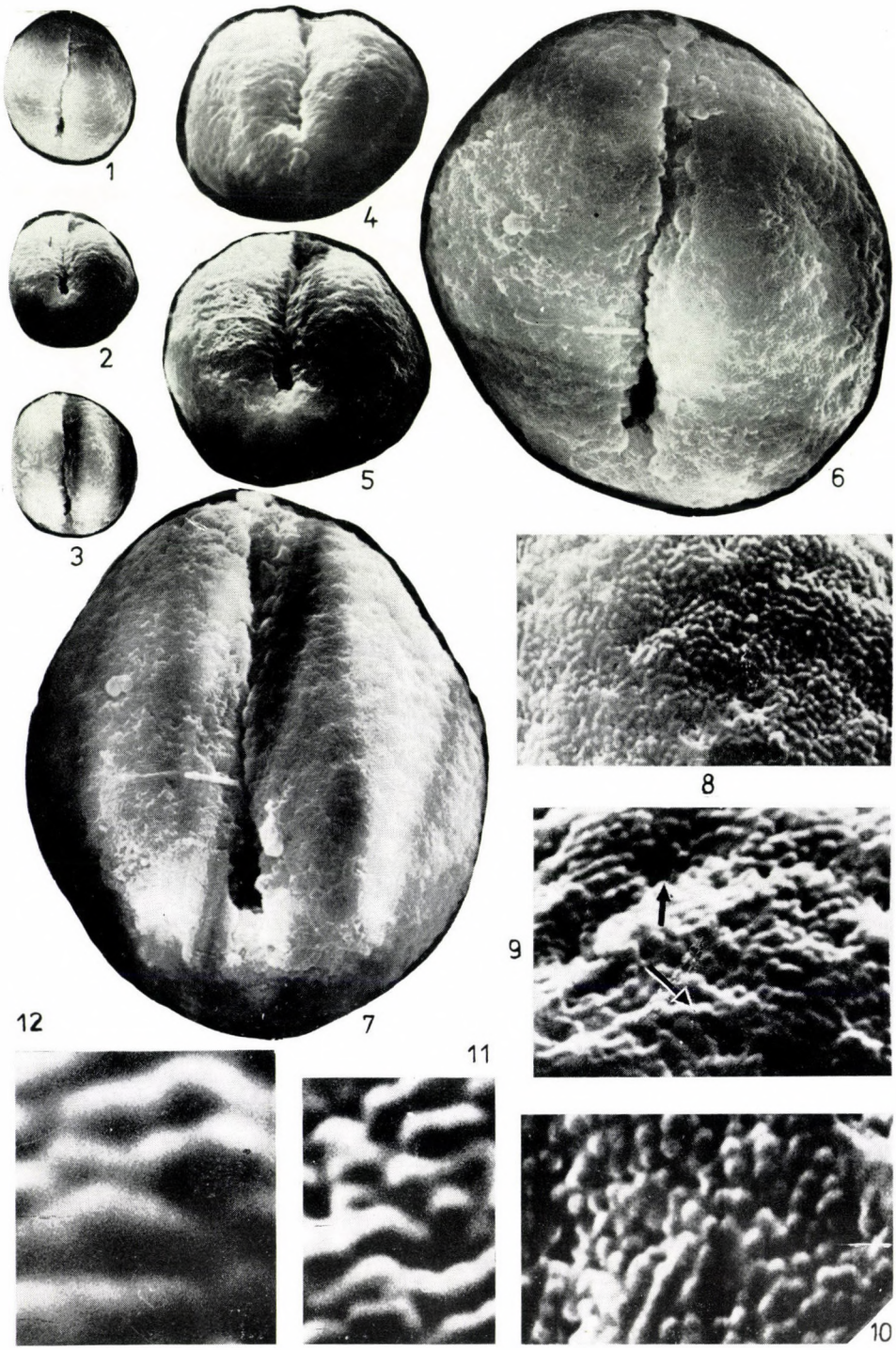
Plate IX, Figs 28–43

Synonym: *Transitoripollis similis* Juhász et Góczán 1976, p. 38, Plate I: 3, 4, 5 (nomen nudum).
Derivatio nominis: similis = Greek for similar, equal. Reference to the resemblance to the type.
Locus typicus: Tés, borehole Tés-27.
Stratum typicum: 50.0 m, grey argillaceous marl, Tés Clay Formation, Middle Albian.
Holotype: grain in slide I/1–2, coordinates 29.3–102.2, Plate IX, Figs 28–33.

Diagnosis: Prolate spheroidal, small-sized, thin-exined, monosulcate pollen grain, circular in shape when viewed in the E-plane.

Plate IX

1–7. *Transitoripollis anulisulcatus* nov. sp. (paratype). Oroszlány, borehole O-1891, 529.1–530.2 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide No. 2, coordinates 20.6–116.1. Light micrographs of paratype, ×1000. 8–14. *Transitoripollis anulisulcatus* nov. sp. (paratype). Pusztavám, borehole Pvt-2, 120.0–121.20 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Single grain preparation, Light micrographs, ×1000. 15–17. *Transitoripollis praesimilis* nov. sp. (holotype). Oroszlány, borehole O-1891. 398.4–398.5 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide 19159/1, coordinates 34.1–124.5. Light micrographs of holotype, ×1000. 18–21. *Transitoripollis praesimilis* nov. sp. (paratype). Tata, borehole Tvg-55, 14.7 m, grey siltstone facies, Vértessomló Siltstone Facies, Lower Albian, tardefurcata-Zone. Grain in slide 40784/1, coordinates 8.0–112.1. Light micrographs of paratype, ×1000. 22–27. *Transitoripollis praesimilis* nov. sp. (paratype). Oroszlány, borehole O-1891, 529.1–530.2 m. Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide No. 2, coordinates 14.3–113.3. ×1000. 28–33. *Transitoripollis similis* nov. sp. (holotype). Borehole Tés-27, 50.5 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide I/1–2, coordinates 8.7–96.1, ×1000. 34–39. *Transitoripollis similis* nov. sp. (paratype). Borehole Tés-27, 50.0 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide T/1–2, coordinates 8.7–96.1, ×1000. 40–43. *Transitoripollis similis* (paratype). Pusztavám, borehole Pvt-2, 120.0–121.20 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide 13948/1, coordinates 15.3–107.2, ×1000. 44–51. *Transitoripollis anulisulcatus* nov. sp. Light micrographs of holotype, ×1000. Oroszlány, borehole O-1891, 529.1–530.2 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. Grain in slide No. 2, coordinates 6.4–108.7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The sulcus extends along the polar axis, is shorter than this, but does not reach the wall, opening equally in both layers of the exine.

The exine is 0.4 to 0.5 μm. It consists of two layers that are more or less equally thick. The nexine is 0.4 to 0.5 μm thick, smooth, unsculptured, with no dissolving field along the sulcus.

The sexine seems to equal the nexine in thickness. Its surface seems to be chagrenate when viewed under light microscope. It is of microverrucate ultrasculpture when studied by SEM.

Size range: Length 16 to 17 μm, width 16 to 17 μm, wall thickness 0.8 to 1.0 μm. Size of holotype 16×16 μm, its wall thickness 1.0 μm, $P/E = 1$, $P/e = 16$.

Differential diagnosis: With its circular outline, size and size ratios and peculiar sulcus, *Transitoripollis similis* nov. f. sp. differs from *Transitoripollis anulisulcatus* nov. f. sp.

Remark: The first representatives of *Transitoripollis similis* nov. f. sp. appear in the upper part of the Vértessomló Siltstone Formation. Their acme falls to the time of birth (Middle Albian) of the Tés Clay Formation, while in the beds assigned to the dispar-Zone of the Upper Albian substage it is only a few specimens of the species that can be encountered.

Transitoripollis praesimilis nov. f. sp.

Plate IX, Figs 17–27

Synonym: *Transitoripollis praesimilis* Juhász et Góczán 1976, p. 38, Plate 1, 2: nec. Pl. 1 : 3 (nomen nudum).

Derivatio nominis: an expression of its relation to similis.

Locus typicus: Oroszlány, borehole O-1825.

Stratum typicum: 398.4–398.5 m, dark grey argillaceous marl, Tés Clay Formation, Middle Albian.

Holotype: specimen in slide 19159/1, coordinates 34.1–124.5, Plate IX, Figs 15–17.

Diagnosis: Small-sized, oblate spheroidal and prolate spheroidal, thin-exined, tectate, monosulcate pollen grain, slightly oval or circular in the E-plane.

Its sulcus extends along the P-axis, reaching normally from wall to wall. The exine has a simple split in both layers. It is 0.8 to 1.0 μm thick, inclined to folding, consisting of two more or less equally thick layers tightly adhering to each other.

Nexine 0.4 to 0.5 μm, smooth, structureless.

Sexine of equal thickness, tectate-perforate. Chagrenate when viewed with a light microscope.

Size range: Length 16 μm, width 14 to 17 μm, wall thickness 0.8 to 1.0 μm, $P/E = 0.94$ to 1.1, P/e 16 to 20. Length of holotype 16 μm, its width 17 μm, its wall thickness 1 μm; $P/E = 0.96$, P/e 16.

Plate X

Transitoripollis sp. (SEMGs from a drop slide). Pusztavám, borehole Pvt-2, 120.0–121.20 m, Munieria-bearing grey argillaceous marl facies, Tés Clay Formation, Middle Albian. SEMGs. 1–3 = ×1000, 4–5 = ×2000, 6–7 = ×3600, 8 = ×10 000, 9 = ×20 000, 10 = ×30 000, 11 = ×60 000, 12 = ×100 000. 1–7. Total images from the sulcal side of the grain, with a sulcus extending from pole to pole. 8–12. Details from the tectate-verrucate surface which is seldom perforated (the arrows indicate the external lumen of the perforation). As can be seen in 10, the verrucae, circa 0.1 μ in diameter, are arranged, as a rule, in groups of four. 11–12 clearly show that the verrucae are coalesced in twos (or threes) along their base

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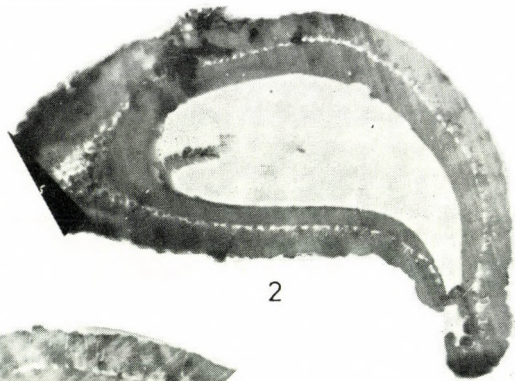

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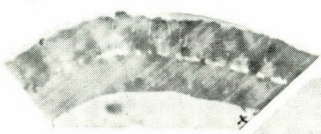

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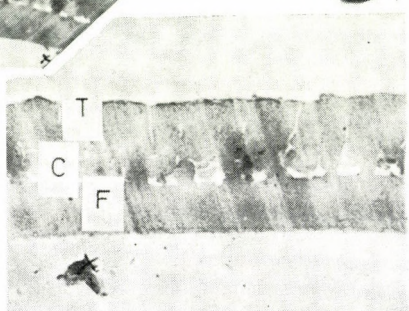

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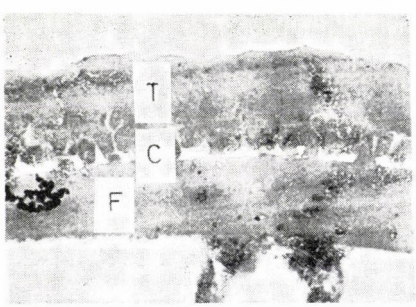

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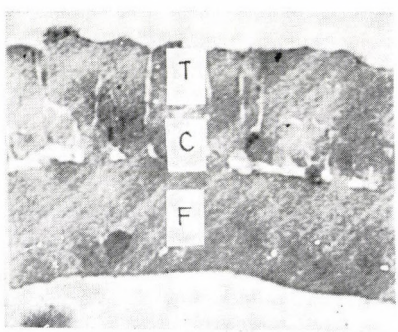

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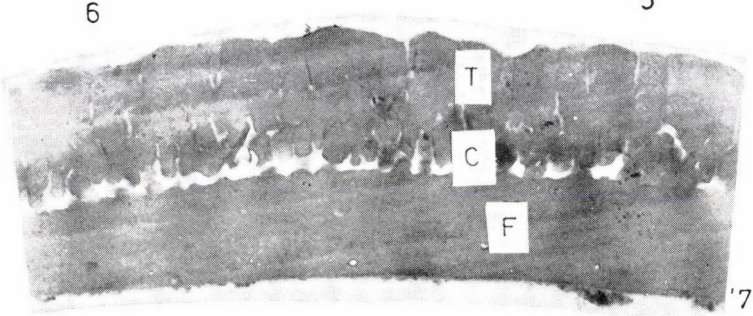

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Differential diagnosis: *Transitoripollis praesimilis* nov. f. sp. resembles most to *T. similis* nov. f. sp. Its outline, however, is usually oval, while that of similis is circular. Its exine is most frequently thinner than that of *T. similis*, therefore it is liable to folding which is not the case with similis. Those are the features that distinguish it from *T. similis* nov. f. sp.

Remark: Its first representatives are found in beds of the Vértessomló Siltstone Formation belonging to the tardefurcata-Zone of the Lower Albian. Their last occurrence is in the upper reaches of the Middle Albian Tés Clay Formation. This is the most ancient angiospermid pollen grain known from the Mesozoic of Hungary.

Subturma: Crassinexines **nov. subturma**

Infraturma: *Crassinexines – Reticulati* **nov. infraturma**

Subinfraturma: Crassinexines – Reticulotrichotomonosulcati **nov. subinfraturma**

Form-genus **Oroszlanyipollis nov. form-genus**

Derivatio nominis: after the type locality—Oroszlány.

Genotype: *Oroszlanyipollis grandis* nov. form-genus et form-species.

Generic diagnosis: Medium-sized to large, thick-exined, tectate-reticulate, trichotomosulcate pollen grain, circular or slightly oval in outline in the E-plane, oblate spheroidal and prolate spheroidal, dorsoventrally-depressed, characterized by a sexine thickness to nexine thickness ratio between 1 : 2 and 1 : 3 and a largest diameter versus wall thickness ratio between 5.6 and 6.2.

Sulcus ramified in Y-shape, reaching from wall to wall and piercing the whole thickness of the exine.

The columella layer of the sexine consists mostly of baculae more than 1 μ high, the tectum is represented by a reticulum resulting from the muri connecting the tips of the baculae. The size of the lumen of the reticulum is nearly equal throughout the surface.

The nexine is thick, smooth, its inner surface being covered by a lamella less than 1 μm thick.

Differential diagnosis: With its characteristic size ratios, its thick exine, its tectate-reticulate sexine and its trichotomonosulcate germinal aperture, *Oroszlanyipollis* nov. form-genus sharply deviates from all known fossil pollen grains deriving from angiospermid plants. From *Similipollis* nov. f. gen., a monosulcate, tectate-reticulate, thick-walled taxon of most similar make-up, it differs primarily by the pattern of the sulcus and the reticulum. In case

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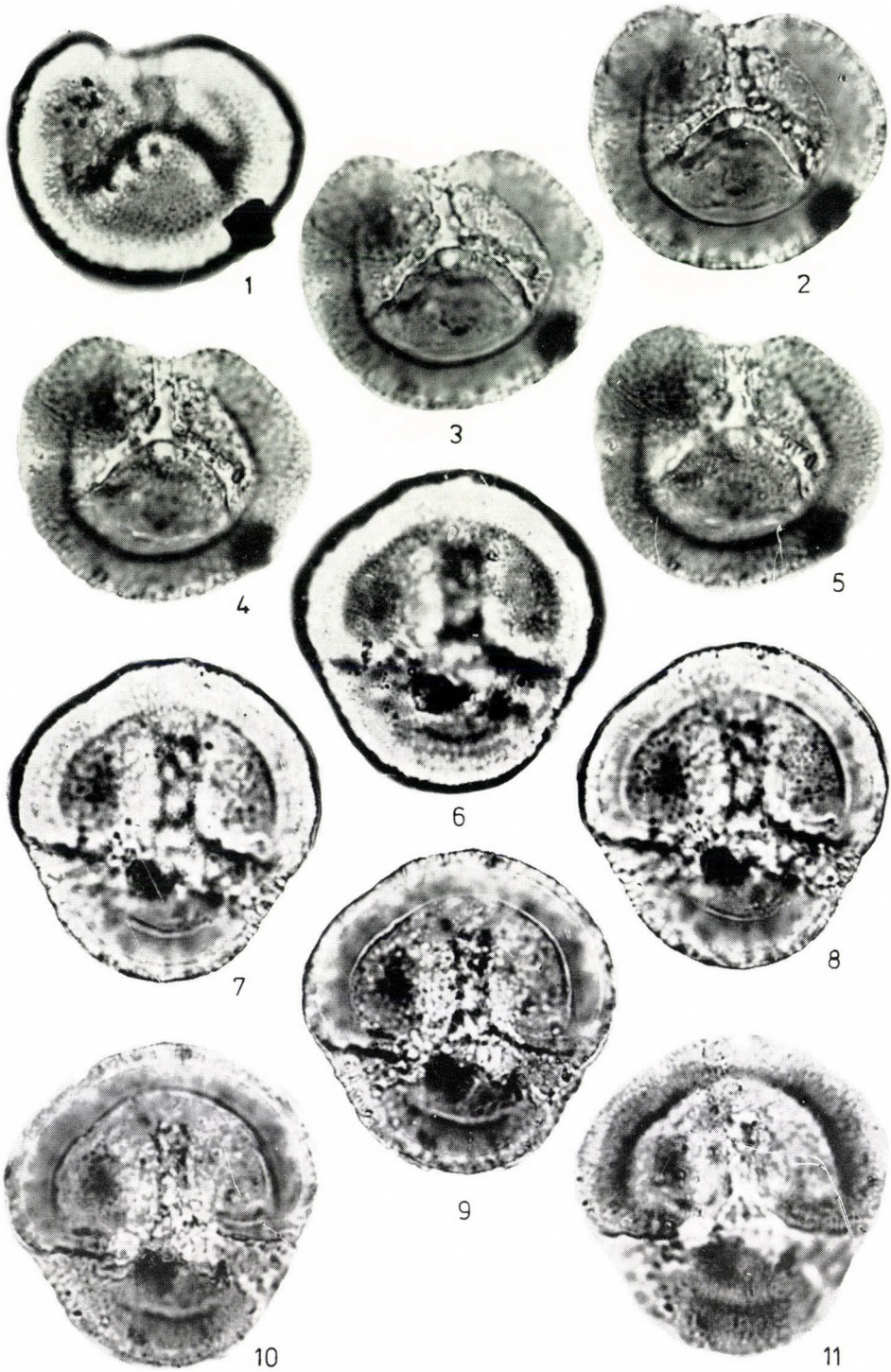
Plate XI

Transitoripollis sp. 1–7. TEMGs. 1, 6. First grain: 1 — subequatorial section (×3000), 6 — detail from the wall of grain 1 (×15 625). The sexine and nexine of equal thickness, the short bacula forming the columella layer of the sexine and the perforate tectum coalesced into a thick, closed layer at the tips of the former can be readily seen. 2. Second grain (×5000), tangential section along the sulcus. 3a–b. Detail from the sulcal section (×6000). That the nexine is thinned along the sulcus can be readily seen (3a). 4. Detail from that part of wall marked with (×14 850). The squat, short, baculate columella and the compact, perforate tectum are quite distinct. 5. Detail from segment 3b. Note the densely perforate tectum and the squat columnar layer of the columella (×20 000). 7. Fourth grain. Detail from the wall. Note the sexine to nexine thickness ratio, the homogeneous nexine, the columella layer of the sexine built up of densely spaced columnar elements and the compact, but finely perforate tectum (×20 000)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of monosulcate *Similipollis* nov. f. gen., the diameter of the lumen of the reticulum forming its tectum at the surface of shell is of strongly different size.

Remark: The first representatives of *Oroszlanyipollis* nov. form-genus are found in the Middle Albian beds of the Tés Clay Formation, its youngest members occurring in the siltstone beds of the Pénzeskút Formation assigned to the Lower Cenomanian mantelli-Zone. Because of its rare, but consistent occurrence, the form under consideration is of chronostratigraphic value.

Oroszlanyipollis grandis n. f. sp.
Plate XII, Figs 1–11

Synonym: *Similipollis grandis* Juhász et Góczán 1976, p. 38, Plate I: 15.
Derivatio nominis: after its large size.
Locus typicus: Oroszlány, borehole O-1825.
Stratum typicum: 220.50 m, grey glauconitic marl, Pénzeskút Marl Formation, Upper Albian, Lower Vraconian, blancheti-Subzone.
Holotype: grain in slide 17353/2, coordinates 31.0–114.4, Plate XII, Figs 1–5.

Diagnosis: Large-sized, suboblate, thick-exined, tectate -reticulate, trichotomosulcate pollen grain, slightly oval in the E-plane. Its sulcus extends from wall to wall, in the sexine there is generally a narrow Y-shaped split, widened in a funnel shape at one of its ends. In the thick nexine it opens more widely and is accompanied radially by a dissected field 2 to 3 micron wide.

The exine is 6 to 8 μm wide, composed quite distinctly of two layers of different structure.

The nexine is 4 to 6 μm thick, smooth, compact, its inner surface being covered by a lamella of 0.5 to 0.6 μm thickness. The opening where the sulcus is pierced is accompanied, in a width of 2 to 3 μm, by verrucae elements resulting from the breakthrough. The sulcus is narrowed at its end widening in the shape of a funnel.

The sexine is 1.8 to 2.2 μm thick, tectate-reticulate. The columella is composed of 1.7 to 2.0 μm high bacula, the tectum consists of muri connecting, in a network pattern the tips of the bacula.

The reticulum covers the entire surface, the diameter of its lumen being more or less equal over the entire surface.

Size range: Length 37 to 43 μm, width 42 to 51 micron, wall thickness 6.8 μm, lumen diameter 0.5 to 1.5 μm, $P/E = 0.84–0.95$; $P/e = 4.6–7.1$. Length of holotype 37 μm, its width 42 μm, its wall thickness 8 μm, lumen diameter of reticulum circa 0.8 μm, $P/E = 0.88$; $P/e = 4.62$.

Differential diagnosis: With its structure, sculpture, size, wall thickness and index values, *Oroszlanyipollis grandis* n. f. sp. is readily distinguished with all known trichotomosulcata species.

Plate XII

1–5. *Oroszlanyipollis grandis* nov. sp. (genotype). Oroszlány, borehole O-1825, 220.5 m, glauconitic marl facies, Pénzeskút Siltstone Formation, Lower Vraconian, blancheti-Subzone. Grain in slide 17353/2, coordinates 31.0–111.4, ×1000. 6–11. *Oroszlanyipollis grandis* nov. sp. (paratype). Oroszlány, borehole O-1825, 220.5 m, glauconitic marl, Pénzeskút Marl Formation, Lower Vraconian, blancheti-Subzone. Photographed from a single grain preparation, ×1000

Subinfraturma: Crassinexines – Reticulomonosulcati nov. subinfraturma

Form genus: **Similipollis nov. f. genus**

Synonym: *Similipollis* Juhász et Góczán 1976, p. 38 (nomen nud.).
Derivatio nominis: similis, greek = similar.
Genotype: *Similipollis varireticulatus* n. f. gen. et n. f. sp.

Generic diagnosis: Medium-sized to large, suboblate, thick exined, tectate-reticulate, monosulcate pollen grain of oval or almost circular outline when viewed in the E-plane, characterized by a sexine thickness to nexine thickness ratio between 1 : 2 and 1 : 3.

The sulcus along the longitudinal axis is mostly represented by a simple split which opens equally in both layers of the exine and forms no radial dissolving field in the nexine.

Exine 4.0 to 4.5 μm thick, composed of a smooth, thicker inner layer and a structured, thinner outer one.

The nexine is 2.5 to 3.0 μm thick, smooth, structureless, the sexine about 1.5 μm, tectate and reticulate. Its columella layer is constituted by bacula of different spacing, its tectum being represented by the muri connecting the external tips of the bacula resulting in a net. The net covers the whole surface, but on the sulcal side the diameter of lumen is smaller than on the opposite one.

Differential diagnosis: The general features and arrangement of the reticulum of *Similipollis* n. f. gen. are similar to the case of *Liliacidites* Couper 1953 from which it deviates, beside its thick exine, by the fact that the diameter of reticulum decreases not from the central field towards the poles, like is the case with *Liliacidites* Couper 1953, but that on the sulcal side there is a reticulum of smaller diameter than on the opposite side. With its shape, size and thick wall it resembles to similarly reticulate, trichotomosulcate *Oroszlanyipollis* n. f. gen. from which its is clearly distinguished both by its simple sulcus and its reticulum of varying lumen. Its species of medium size are similar to Retimonocolpites Pierce 1961 from which it differs quite distinctly by its thick exine and the arrangement of the reticulum.

Remark: The first representatives of *Similipollis* nov. form-genus are found in the lower glauconitic marl beds of the Pénzeskút Siltstone Formation, i.e. in the substuderi Zone of the Upper Albian, its last specimens being encountered in the siltstone beds, assigned to the Lower Cenomanian mantelli-Zone, of the same formation.

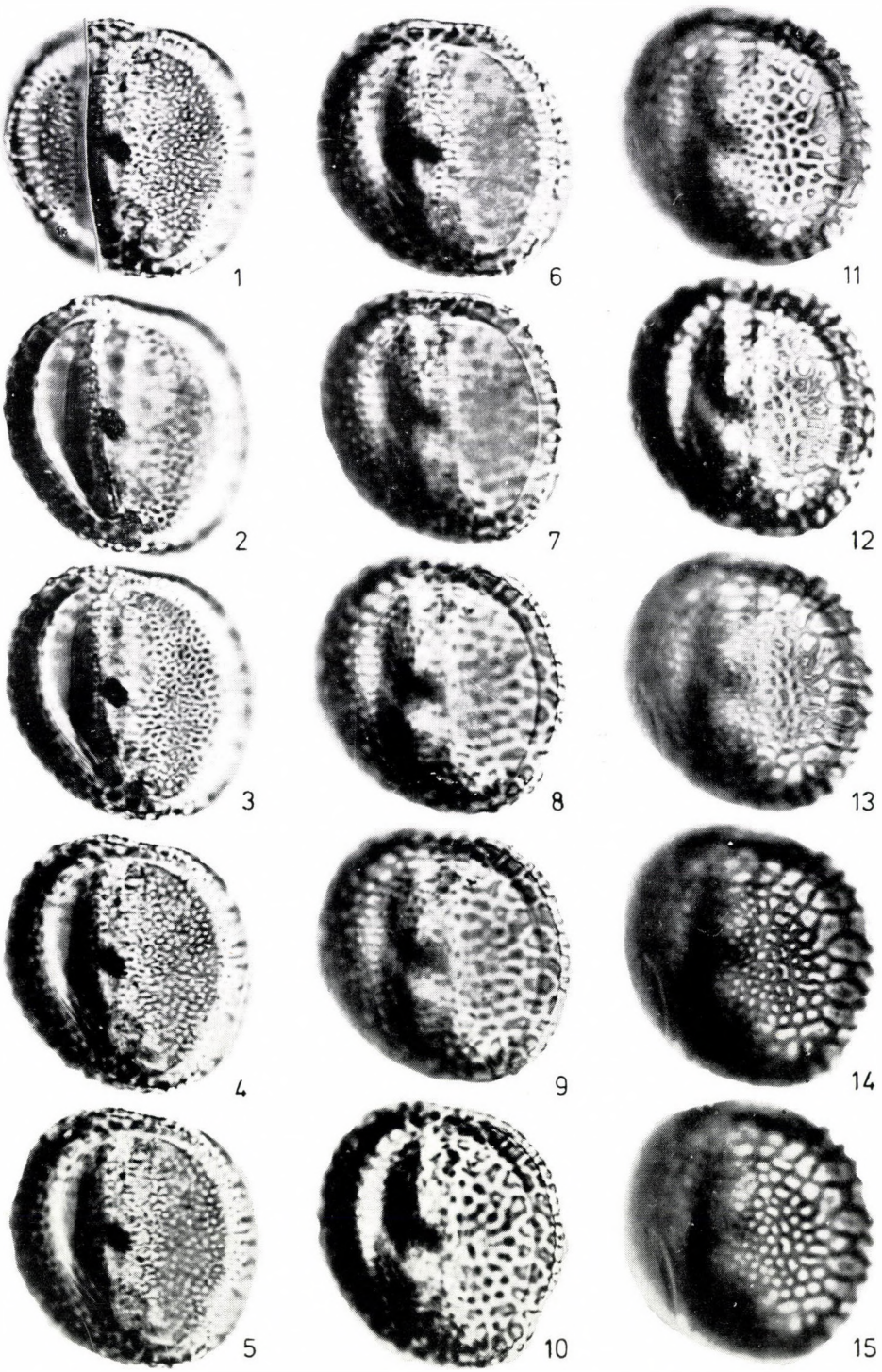
Its acme can be placed in the dispar-Zone of the Upper Vraconian substage. Although unfrequent, but consistent in its vertical range, the new form-genus under consideration may be regarded as being of chronostratigraphic value.

Similipollis varireticulatus nov. f. sp.
Plate XIII, Figs 1–15

Synonym: *Similipollis varireticulatus* Juhász et Góczán 1976, p. 38, Plate 1: 16 (nomen nudum).
Derivatio nominis: after its lumen of varying diameter.
Locus typicus: Pere, borehole Pe-31.

Plate XIII

1–15. *Similipollis varireticulatus* nov. sp. (genotype). Pere, borehole P-31, 191.3–198.3 m Turrilites Marl, Pénzeskút Siltstone Formation, Upper Albian dispar-Zone, bergeri-Subzone Grain in slide 408. coordinates 91–106.2. Light micrographs of genotype, ×1000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Stratum typicum: 191.3–198.3 m, grey marl, Pénzeskút Marl Formation, Lower Cenomanian, mantelli-Zone.

Holotype: grain in slide 408/1, coordinates 9.1–106.2, Plate XIII, Figs 1–15.

Diagnosis: Tectate-reticulate, monosulcate pollen grain of medium size and thick exine, oval or almost circular, suboblate, as viewed in the E-plane.

Its sulcus represents a simple split extending from wall to wall in the longitudinal axis, its ends are usually tapering, while its median shows a kind of convexity on its run.

Both layers of the exine are pierced in a similar way and no dissolving field is formed in the nexine.

The exine is 4 to 4.5 μm thick, composed of a thicker, smooth inner layer and a thinner reticulate outer one.

The nexine is 2.5 to 3.0 μm in size, smooth, unsculptured, the sexine being 1.2 to 2.0 μm, tectatereticulate. The columella layer consists of bacula emerging 0.8 to 1.2 μm high above the nexine, bacula that are shorter on the sulcal side and more densely spaced than it is the case on the opposite side. The tectum, in turn, is formed of 0.4 to 0.8 μm thick muri that are sitting at the outer ends of the bacula and that connect these into a net. The reticulum is of irregular shape and of varying size showing a lumen diameter that is smaller on the sulcal side than it is on the opposite one.

Size range: Length 31 to 36 μm, width 35 to 38 μm, wall thickness 4.0 to 4.5 μm, $P/E = 0.88$ to 1.1; $P/e = 7.7$ to 9.2.

Length of holotype 37 μm, its width 35 μm, its wall thickness 4 μm, $P/E = 1.1$; $P/e = 9.2$; sexine to nexine ratio = 1.5 to 2.5.

Differential diagnosis: With the peculiar features of the reticulum and the arrangement of the diameter of lumen of the reticulum, *Similipollis varireticulatus* nov. f. sp. deviates quite distinctly from the hitherto-known reticulate, monosulcate species.

Remark: The representatives of *Similipollis varireticulatus* have been recovered from the Upper Albian (Upper Vraconian) dispar-Zone of the Pénzeskút Siltstone Formation up to the Lower Cenomanian mantelli-Zone of the same formation, its acme being seemingly in the dispar-Zone.

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MORFOLOGÍA DE LOS GRANOS DE POLEN DE LAS CHLORANTHACEAE Y CANELLACEAE CUBANAS

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(Recibido: 15 Mayo 1983)

Pollen morphology of the families Chloranthaceae and Canellaceae of Cuban plants are described in order to see its relations with the primitive Angiosperms.

Introduccion

En este trabajo se describen los tipos de pólenes de las familias Chloranthaceae y Canellaceae. La familia Chloranthaceae con 3 géneros y cerca de 40 especies, está representada en la Flora de Cuba solo por el género *Hedyosmum* con 6 especies, de ellas 5 endémicas. La familia Canellaceae con 5 géneros y 6 especies, está representada en Cuba por los géneros *Canella* y *Cinnamodendron* con una especie en cada uno de los géneros mencionados, siendo la especie *Cinnamodendron cubense* Urb.

En la actualidad estas familias son incluídas en el grupo de las Angiospermas primitivas. La morfología del polen de las especie de las familias Chloranthaceae y Canellaceae ha sido estudiada en algunos países. En este artículo se hace el estudio de la morfología del polen de 6 especies cubanas de estas dos familias, para observar las relaciones de dichas familias con las Angiospermas primitivas.

Material y metodo

Esta investigación se realizó con las preparaciones de polen de la Esporoteca del Instituto de Botánica de la Academia de Ciencias de Cuba. Todo el estudio del grano de polen se realizó mediante un microscópio óptico Amplival. Las fotografías de los granos de polen se realizaron en diferentes secciones ópticas; detalles de la superficie del grano fueron realizados mediante el empleo del microscópio electrónico de barrido (SEM). La terminología utilizada en este trabajo es la seguida por ERDTMAN.

Relación de las especies estudiadas

CHLORANTHACEAE

1. *Hedyosmum crassifolium* Urb., prov. Ote., ALAIN 5813 LS.
2. *H. grisebachii* Solms., Gran Piedra, prov. Ote., STUCHLIK y MONCADA 789 HAC.
3. *H. leonis* Marie Vict., S. de Nipe, prov. Ote., LEÓN y M. VICTORIN 19964 SV.
4. *H. nutans* Sw., S. de Nipe, prov. Ote., ALAIN y ACUÑA 8021 SV.

CANELLACEAE

5. *Canella winterana* (L.) Gaertn., Stgo de Cuba, Ote., L. FIGUEIRAS 2747 SV.
6. *Cinnamodendron cubense* Urb., prov. Ote., M. CURBELO 15997 SV.

Descripciones de los granos de polen

Hedyosmum grisebachii. Granos de polen monosulcados, ovales hasta esferoidales desde 20–34 × 17–28 μm de diámetro. Los sulcos irregulares, ocasionalmente divididos en dos o tres partes, semejantes como en granos bi- o tricolpados o trichotomosulcado.

Exina 2.2–3.1 μm de grosor, sexina mas gruesa que la nexina desde 1.2 hasta 1.8 μm de grosor; tectada. Testum muy fino, liso, irregularmente ondulado, intrapuntado, soportado por columelas finas de ca. 0.5 μm de diámetro.

Las columelas ocasionalmente reunidas en dos o mas, densamente e irregularmente agrupadas. El espacio entre las columelas desde menos de 0.5 μm hasta 1 μm.

H. leonis. Granos de polen irregularmente aperturados, ovales hasta esferoidales desde 26–34 × 21–32 μm de diámetro. Las aperturas irregularmente desarrollados como monosulcados hasta policolpoidados. Se pueden observar todas las formas intermedias de apertura entre sulcados y policolpados.

Exina 2.2–3.0 μm de grosor, nexina mas o menos del mismo grosor que la sexina; tectada. Tectum muy fino, irregularmente supragranulado, intrapuntado, soportado por columelas muy finas, menos de 0.5 μm de diámetro con interconecciones que asemejan a un retículo. Columelas densamente agrupadas, el espacio entre ellas ca. 0.5 μm.

H. crassifolium. Granos de polen monosulcados, ovales hasta esferoidales desde 25–33 × 19–33 μm de diámetro. Los sulcos irregulares, ocasionalmente divididos, semejantes a granos trichotomosulcados o polisulcados (policolpados).

Exina cerca de 2.5 μm de grosor, nexina del mismo grosor que la sexina; tectada. Tectum muy fino, liso, intrapuntado; soportado por finas columelas de ca. 0.5 μm de diámetro, densamente agrupadas. El espacio entre las columelas más o menos 1 μm. Las columelas ocasionalmente reunidas de dos o tres.

H. nutans. Granos de polen monosulcados, ovales hasta esferoidales, desde 24–36 × 22–34 μm de diámetro. Los sulcos irregulares, ocasionalmente divididos como en granos bi- o trichotomosulcado o colpoidados.

fino, liso o irregularmente supragranulado, intrapuntado, soportado, por columelas finas, de menos de 0.5 μm de diámetro. Las columelas con muy finas interconecciones formando un retículo (reticulum like pattern). El espacio entre las columelas cerca de 0.5 μm.

Canella winterana. Granos de polen monosulcados, ocasionalmente trichotomosulcados, ovales con el diámetro longitudinal de 50–65 μm.

Exina desde 2.4–2.8 μm de grosor, sexina mas gruesa que nexina desde 1.4–2.0 μm de grosor; semitectada, reticulada. Retículo heterobrochado con lúminas más o menos regulares de 0.5–1.0 μm de diámetro. Los muros de 0.5 μm de ancho soportado por finas y bien definidas columelas de menos de 0.5 μm de diámetro.

Cinnamodendron cubense. Granos de polen monosulcados, ovales hasta esferoidales con el diámetro longitudinal de 23–30 μm.

Exina cerca de 1.4 μm de grosor, sexina más gruesa que la nexina (hasta 0.9 μm). Sexina semitectada, reticulada. Retículo heterobrochado con lúminas de menos de 1 μm de diámetro. Los muros ocasionalmente fragmentado, soportado por columelas muy finas, de menos de 0.5 μm de diámetro.

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ADHESION AND GERMINATION OF DIFFERENTLY TREATED MAIZE POLLEN GRAINS ON THE STIGMA

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Maize pollen can only be stored successfully at —196 °C or —75 °C if the water content of the pollen is previously reduced by drying to an adequate extent. Due to the effect of water loss, the membranes of the vegetative cells of the pollen become dehydrated. If the maize pollen loses 65–75% of its original water content in the course of drying, the pollen grains are capable of rehydration and of developing pollen tubes of normal length when placed on the surface of the stigma after drying and storage. It was found, however, that a longer period is required for the pollen grains to adhere to the stigma surface and to begin to form pollen tubes after drying and deep-freezing, than for fresh pollen. Pollen tube formation is delayed and the rate of growth is also slower in the first two hours after pollination when fertilisation is carried out with dried or stored pollen. Therefore, when stored pollen is used for crossing, special attention should be paid to the circumstances under which pollination takes place.

Introduction

Maize pollen, which is by nature short-lived, can be successfully stored at —76 °C or —196 °C for more than a year if the originally high (40–60%) water content is reduced to an adequate extent by gentle drying (BARNABÁS and RAJKI 1981).

Drying is a critical process for the pollen grains: as many authors have reported (KNOWLTON 1922, HOLMAN and BRUBAKER 1926, BAIR and LOOMIS 1941, HOEKSTRA and BRUINSMA 1975), there is a close correlation between the water content and the viability of cereal pollen. As a result of a reduction in the water content of the pollen, the life processes are inhibited, and if this inhibition is not reversible, drying leads to a loss of viability in the pollen grains. HESLOP-HARRISON (1979a, b) observed that more time was required for regeneration on the surface of the stigma in the case of dry rye pollen grains with a water content of 15–20% than for pollen grains with a higher water content; electron microscope examinations demonstrated that the membranes of partially dehydrated rye pollen grains are capable of regeneration on the surface of the stigma, that is the physiological processes retain their reversibility.

In the course of maize pollen storage experiments it has been found that before deep-freezing the pollen must be dried until the water content is approximately 30% of the original water content. This means an actual water content of 15–20% in terms of the fresh weight of the pollen. This low water content eliminates mechanical damage to the membranes due to the formation of ice crystals during sudden cooling to extremely low temperatures.

The aim of the present experiments was to discover how the pollen treatments (drying, deep-freezing) used by the authors influenced the behaviour of the pollen grains on the stigma in the case of artificial pollination.

Materials and methods

Maize pollen with a high water content when fresh, which had been dried to a water content of 15–20%, then stored in liquid nitrogen at −196 °C for various lengths of time, was used as the experimental material. Pieces of stigma approximately 20 mm in length were cut from the mature female inflorescence and pollinated with the pollen under investigation. The pieces of stigma were then placed on slides in a crop of saccharose solution containing agar. The slides were put into Petri dishes in a saturated atmosphere and the pollinated pieces of stigma were incubated in this optimum environment at room temperature for 15, 30, 60 or 120 min. Samples fixed at various times were stained with cotton blue according to D'SOUZA's (1972) method, then the number of pollen grains which had adhered to each piece of stigma during the incubation period was counted, the % pollen tube formation was calculated and the lengths of the pollen tubes which had penetrated most deeply into the style were measured with the aid of an ocular micrometer. The data of 50 experiments were averaged.

The fine structure of pollen grains dried and stored by deep-freezing and of those which were rehydrated on the surface of the stigma and produced pollen tubes was examined using an electron microscope. The material was prepared by fixation in 5% glutaraldehyde for an hour, then in 2% osmium tetroxide, also for an hour at room temperature, after which it was embedded in araldite in the manner usual when applying ultramicrotechniques. The ultra-thin sections were examined with a (Tesla BS-500) transmissional electron microscope.

Results and discussion

The results of the examinations show that the pollen treatments (drying and freezing) influenced processes taking place on the stigma after pollination.

The data in Table 1 demonstrate that 15–30 min. after pollination a relatively large number of fresh pollen grains had adhered to the stigma and developed pollen tubes, whereas for pollen grains dried to a water content of 15–20% the number which had adhered to the stigma and produced pollen tubes was fewer and the rate of pollen tube growth was also slower in the first 30 min. after pollination. The tube formation of maize pollen grains stored in liquid nitrogen did not commence until almost an hour after pollination, and the pollen tube which penetrated most deeply into the tissues of the style

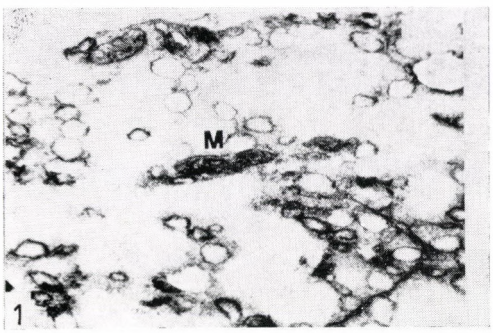
Table 1

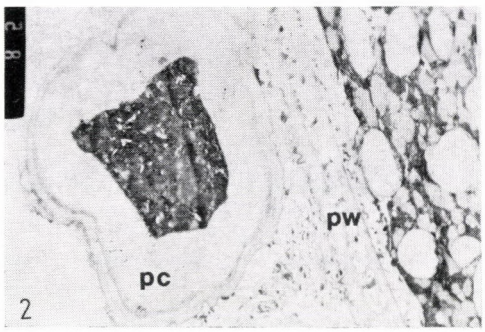
Behaviour of fresh, dried and stored maize pollen grains on the stigma after artificial pollination

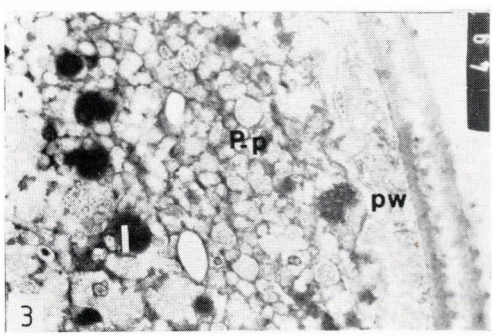
	Incubation period (min)											
	15			30			60			120		
	F	D	S	F	D	S	F	D	S	F	D	S
Number of pollen grains	11	1	—	28	2	—	36	8	3	51	30	18
Germination (%)	57	10	—	73	17	—	87	63	61	84	84	62
Max. lengths of pollen tubes (mm)	0.1	0.03	—	0.6	0.2	—	4.6	1.6	0.9	13.8	8.6	6.1

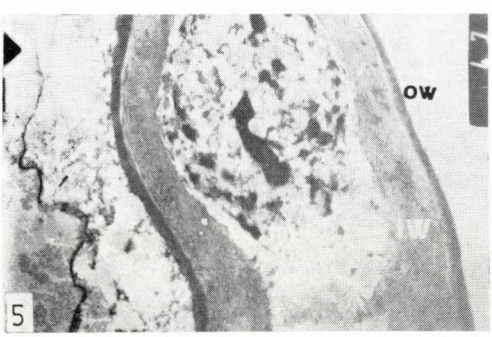
F = fresh pollen
D = dried pollen
S = stored pollen

was only half the length of that measured after pollination with untreated pollen. Even two hours after the pollen grains were placed on the stigma, there were still considerable differences between the variants in the lengths of the pollen tubes.









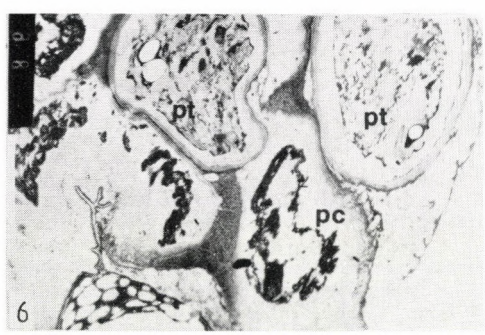


Fig. 1. Cytoplasm in the vegetative cell of a pollen grain stored in the dehydrated state. Magnification: ×18 200. m = mitochondrium

Fig. 2. Adhesion of a pollen grain to the stigma papilla. Magnification: ×6000. pc = papilla cell, pw = pollen wall

Fig. 3. Rehydrated pollen grain on the stigma. Magnification: ×6000. P-p = polysaccharide particle, l = lipid droplet, pw = pollen wall

Fig. 4. Initiation of pollen tube formation. Magnification: ×1000. ptw = pollen tube wall

Fig. 5. Longitudinal section of a growing pollen tube. Magnification: ×1000. ow = outer wall, iw = inner wall

Fig. 6. Cross-section of pollen tubes growing in the intercellular spaces of papilla cells. Magnification: ×4000. pt = pollen tube, pc = papilla cell

In the electron microscope pictures the plasma membranes in the vegetative cells of partially dehydrated, deep-frozen maize pollen grains can hardly be distinguished and the cell organelles are difficult to identify (Fig. 1). After the pollen grains have rehydrated and adhered to the stigma (Fig. 2), reorganisation takes place in the cytoplasm. Polysacchaside particles and lipid droplets are visible (Fig. 3) and the formation of pollen tubes begins (Fig. 4). The wall of the initiating pollen tube consists of cellulose microfiber bunches embedded in a matrix material. Later the pollen tube wall becomes bi-layered. It has an inner callosic and an outer cellulosic region (Fig. 5). The growing pollen tubes progress along the intercellular spaces between the papilla cells of the stigma towards the vascular tissue system (Fig. 6) in the style.

The results of the examinations show that maize pollen is able to survive a decrease of approx. 70% in its original water content. The effect of storing by drying and subsequent deep-freezing was apparent in the longer period required for the regeneration of the pollen grains on the stigma and in the slower growth of the pollen tubes in the first 1–2 hours after pollination compared to that of fresh pollen. The further organisation of tube growth was quite normal. These findings confirm the observations of HESLOP-HARRISON (1979a, b) who stated that it takes a considerable time for partially dehydrated cereal pollen to adhere to the style.

Since at least an hour is required on the stigma for the full regeneration of maize pollen grains which have survived storage, environmental factors have a greater influence on the success of pollination.

Thus, if stored pollen is to be used for crossing, great care must be taken to carry out the artificial pollination under optimum environmental conditions.

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XYLOTOMIC EXAMINATIONS OF SOME VENEZUELAN SPECIES OF THE CAPPARIDACEAE I

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Authors make known the exterior morphological and ecological characteristics, habitat, moreover the main anatomical features of the xylem of two Venezuelan Capparidaceae species, namely *Steriphoma elliptica* Spreng. and *Belencita nemorosa* (Jacq.) Dugand.

Materials and methods

The blocks made from the wood of the two species were softened in the mixture of water and glycerin, in a BRINZER's autoclave, at 1.5–2.0 atm., and then transversal, tangential and radial sections were prepared. The sections were dyed with the alcoholic solution of Toluidin-blue. The maceration of tissues was made with the SCHULZE-method (SÁRKÁNY and SZALAI 1964).

Length of fibres and vessel-elements, tangential and radial diameters of vessels, width and height of medulary rays and other characteristics were calculated from 50–100 measurements. Enlarged microphotographs were made on each section.

External morphology and distribution on the basis of description made by Prof. I. R. BERMUDEZ and Prof. L. J. CUMANA.

External morphology

Steriphoma elliptica Spreng.

Tree or shrub 1–5 m. Stem pilose (or hirsute), lanuginous. Leaves: simple alternate coriaceous and concoloured. Plate 2–14 cm long, oblong-lanceolate, its base obtuse, the end in short apex. Inflorescence racemose, terminal, adhereing to the branch with a 4–8 cm long peduncle (Fig. 1). Flowers hermaphrodite, actinomorphic, 7–10 cm long. Calyx with 4 sepals, 1.5–2 cm long covered with glossing beard. The 4 opposite petals are erect and yellow Number of stamina 6–7, 6–7 cm long, lower part of filament covered with beard. Anthers 4–6 mm long, oblong, dehiscence longitudinal. Pistil 0.5–1.5 mm long, style 0.5–7.5 cm long, ovary with two carpels, with pseudoseptum of one or two dissepiments. Ovula numerous, placenta parietal. Fruit berry, gently oval, pedunculated; surface wrinkled and covered with scaly hairs, pubescent, light chestnut-coloured.

Habitat: oligotrophic, dry, gravelly and sandy soils. Grows isolated along ways, on bluff (sheer, bold) embankments and hilly countries.

Distribution: in Venezuela, State Anzoátegui, Nueva Esparta, in States Sucre and Trujillo.

Fig. 1. Steriphoma elliptica Spreng. Leaves and inflorescence. Photo and collector: I. BERMUDEZ and L. CUMANA, Edo. Sucre, 2. 6. 1983

Fig. 2. Belencita nemorosa (Jacq.) Dugand. Shrub, habitat. Photo and collector: I. BERMUDEZ and L. CUMANA, Edo. Sucre, 2. 6. 1983

Fig. 3. Belencita nemorosa (Jacq.) Dugand. Flower and leaves. Photo and collector: L. G. GONZÁLES, Edo. Sucre, 10. 2. 1983

Fig. 4. Belencita nemorosa (Jacq) Dugand. Leaves and seeds. Photo and collector: I. BERMUDEZ and L. CUMANA, Edo. Sucre, 2. 6. 1983

Belencita nemorosa (Jacq.) Dugand

Shrub or tree, 2–4 m high (Fig. 2). Young stem pubescent. Leaves simples, alternates, coriaceous and concolourous, oval and oblong-shaped, almost cordate at the base acuminate at the apex. Edge of limb scarcely undulated. Terminal flowers hermaphrodite, actinomorphic. Calyx with 2–3 sepals, 2.5–5 cm long, chestnut coloured and covered with shiny hairs. Corolla with 6 petals, 4 of them of same length (4–4.5 cm), but 2 are only 0.8–1.1 cm long. Stamina 16, 2.5 cm long. Anthers bitheca, 0.6–1.1 mm long, dehiscence longitudinal. Pistil 5–7 mm long, with a superior ovary bicarpel, 1- or 2-celled divided by a pseudoseptum. Ovules numerous, placentation parietal. Fruit berry, oblong-oval, pedunculated, smooth, olive-green and shiny (Figs 3 and 4).

Habitat: in dry, rocky olygotrophic soils. Frequent along ways and footpaths. Grows usually solitary, forms rarely stands.

Distribution in Venezuela: in State of Anzoátegui, Falcón, Lara, Monagas, Sucre Trujillo and Zulia.

Wood anatomy

Steriphoma elliptica Spreng.

Diffused porous wood. The basic mass of the wood is formed by polygonal shaped fibres with thinner wall and wide lumen. Aliform confluent and contact-vasicentric longitudinal parenchyma (METCALFE and CHALK 1950). Medullary rays one- and very rarely two cells wide (Fig. 5). Growing zones of the wood are recognizable. Oval-shaped tracheae, tangentially flattened within the groups (2–4–16 members), 16–28–45 tracheae per mm^2. Tangential diameter 37.2–51.1–69.7 μm. Length of the vessel-members 69.0–250.7–368.0 μm, alternate, moderate-sized bordered pits on their wall. In tracheae rarely mastic material. Simple perforation plate.

Medullary rays 1 cell wide, very rarely 2 cells wide, with homogeneous structure. Height 74.4–168.6–325.2 μm. Width 9.3–11.3–13.9 μm. Ray cells not rarely contain mastic material (Figs 6 and 7).

Fibres are arranged in radial rows. Diameter 6.9–12.6–20.7 μm. Wall thickness constantly 2.3 μm. Full length 710.0–564.4–923.0 μm. Tip of the fibres usually plain running in short apex, rarely ramified and sometimes one of the tips is serrated. Diameter of the longitudinal parenchyma cells up to 9.3–14.9–18.6 μm. Height 51.1–94.3–125.5 μm.

Belencita nemorosa (Jacq.) Dugand

Diffused porous wood. The basic mass of the wood is formed by fibres of thinner wall and middle lumen. Paratracheal, contact-vasicentric longitudinal parenchyma. Medullary rays one-two and three cells wide (Fig. 8). Roundish or oval-shaped tracheal, flattened tangentially, within the groups (2–4–8 members) 23–33–40 trachea per mm^2. Tangential diameter 32.5–51.5–69.7 μm. Radial diameter 46.5–58.1–74.4 μm. Length of the vessel-members 92.0–177.5–230.0 μm and alternate, moderate-sized elongated bordered pits on their wall. Simple perforation plate.

Medullary rays 1–2, not rarely 3 cells wide, with heterogeneous structure. Height 141.0–216.0–1230.5 μm. Width 11.5–23.0–34.5 μm (Figs 9 and 10).

Fibres are arranged in radial rows. Diameter up to 11.5–16.1–20.7 μm. Wall thickness 2.3–4.6 μm. Full length 710.0–539.6–923.0 μm. Tip of the fibres ending in plain apex, sometimes serrate.

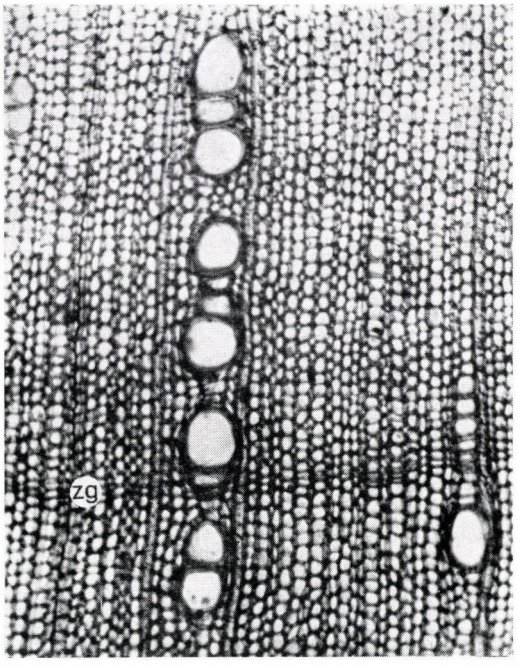

Fig. 5. Steriphoma elliptica Spreng. Cross-section ×120. vessels, Vessel-groups, medullary rays and fibres. Contact-vasicentric and aliform-confluent longitudinal parenchyma. zg = zone of growth

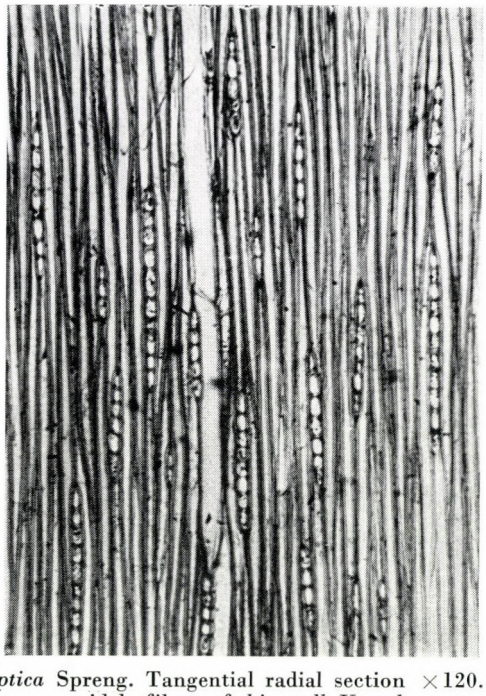

Fig. 6. Steriphoma elliptica Spreng. Tangential radial section ×120. Ray cells of one cell width, fibres of thin wall. Vessel

Fig. 7. Steriphoma elliptica Spreng. Radial longitudinal section ×120. Homogeneous rays, longitudinal parenchyma and fibres

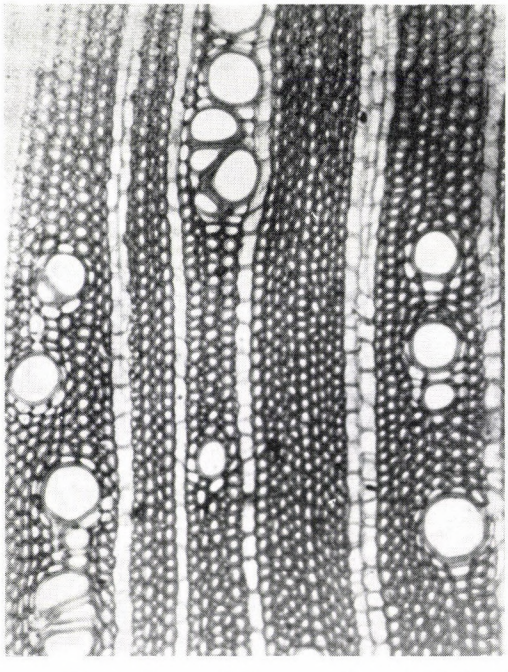

Fig. 8. Belencita nemorosa (Jacq.) Dugand. Cross-section ×120. Small sized vessels, vessel-groups, medullary rays and fibres. Contact-vasicentric longitudinal parenchyma

Fig. 9. Belencita nemorosa (Jacq.) Dugand. Tangential longitudinal section ×120. Medullary rays with one-two-three cells in width, fibres of thick wall and vessels

Fig. 10. Belencita nemorosa (Jacq.) Dugand. Radial longitudinal section ×120. Heterogeneous medullary rays, fibres, vessels and contact-vasicentric longitudinal parenchyma

Table 1

Anatomical features of the species examined

Wood elements	Features	*Steriphoma elliptica*	*Belencita nemorosa*
Trachea	arrangement	diffused, solitary or in radial groups of 2–4–16 members	diffused, solitary or in radial groups of 2–4–8 members
	shape	oval-shaped within the groups tangentially flattened	roundish or oval shaped in groups in tangential direction flattened
	tangential diameter	37.2–51.1–69.7 μm	32.5–51.5–69.7 μm
	radial diameter	32.5–57.3–69.7 μm	46.5–58.1–74.4 μm
	length of vessels	69.0–250.7–368.0 μm	92.0–177.5–230.0 μm
	number per mm^2	16.0–28.2–45.0	23.0–33.4–40.0
	wall thickness	2.3–3.2–4.6 μm	4.6–5.6–6.9 μm
	intervascular pitting	bordered	elongated bordered
	perforate plate	simple	simple
	content	rarely mastic material	—
Medullary rays	width	narrow	wide
	number of cells	1, rarely 2	1–2 or 3
	classification	homogeneous	heterogeneous
	height	74.4–168.6–325.2 μm	141.0–216.0–1230.6 μm
	width	9.3–11.3–13.9 μm	11.5–23.0–34.5 μm
	content	mastic material	—
Fibres	arrangement	in radial rows	in radial rows
	shape	polygonal	polygonal
	full diameter	6.9–12.6–20.7 μm	11.5–16.1–20.7 μm
	wall thickness	2.3 μm	2.3–4.6 μm
	full length	710.0–564.4–923.0fμm	710.0–539.6–923.0 μm
	type of pitting	with split	small, with split
Longitudinal parenchyma	arrangement	contact-vasicentric and aliform-confluent	contact-vasicentric
	diameter	9.3–14.9–18.6 μm	4.65–10.9–18.6 μm
	height	51.1–94.3–125.5 μm	37.2–67.2–111.6 μm
	number of cells	2–4	2–4–6
	content	—	—
	other	—	—

Diameter of the longitudinal parenchyma cells up to 4.65–10.9–18.6 μm. Height 37.2–67.2–111.6 μm. The detailed anatomic features of the wood of the two species are summarized in Table 1.

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CUTICULAR ANALYSIS OF THE LEAF OF *CERATOPYXIS VERBENACEA* (GRISEB.) HOOKER F. EX HOOKER (RUBIACEAE)

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The main leaf epidermal characters of taxonomic significance in *Ceratopyxis verbenacea* (Griseb.) Hooker f. ex Hooker are described, by the use of light and scanning electron microscopes.

Introduction

Ceratopyxis is a monotypic endemic genus of the limestone "haystack-hills" of West Cuba. The species *Ceratopyxis verbenacea* (Griseb.) Hooker f. ex Hooker was founded by HOOKER F. (1872) on the basis of the GRISEBACH's species *Rondeletia? verbenacea.*

This shrub belongs to the tribe Chiococceae of the Rubiaceae family. It is a resiniferous unarmed tall shrub or little tree up to 4–6 m height. The leaves are opposite and coriaceous.

BORHIDI (1973) and in: VALES, BABOS, BORHIDI 1977 pointed out that this shrub is one of the most important element in the pioneer phase of the limestone rock series succession of the haystack-hills. It can be found sparsely in the fissure of perpendicular insolated slopes and as a dominant species at the uppermost part of the mogotes.

In this paper, the leaf epidermal features of this genus were studied by the biological and scanning electron microscopes in order to contribute to increase the knowledgment of this species and to find another features of affinities with other genera.

Material and methods

Mature leaves from the herbarium of the Institute of Botany of the Academy of Sciences of Cuba (HAC) were taken for this research.

A small portion of the middle part of the leaf, including margin, adaxial and abaxial surfaces, were macerated by boiling in a solution of 30% hydrogen peroxide and glacial acetic acid in relation 1 : 1. The cuticle obtained was washed and stained with a 2% aceto-orcein solution, and mounted in glycerin-jelly.

The observations and photographs with the scanning electron microscope were realized from gold coated samples in a Cambridge Instrument (Stereoscan S4-10).

Results

Single unicellular and conical hairs present on adaxial and abaxial surfaces (Figs 1 and 2). The trichomes are raised (Figs 3 and 4) and show wide rounded basis. Hair's frequency more or less the same in both surfaces, only greater on the veins. Epidermis formed by only one layer of cells. Epidermal

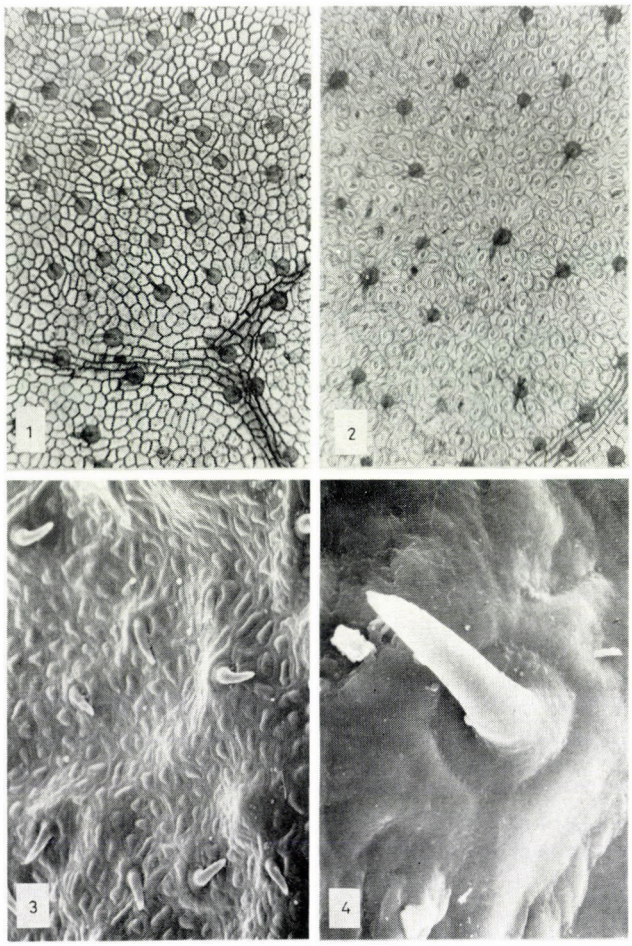
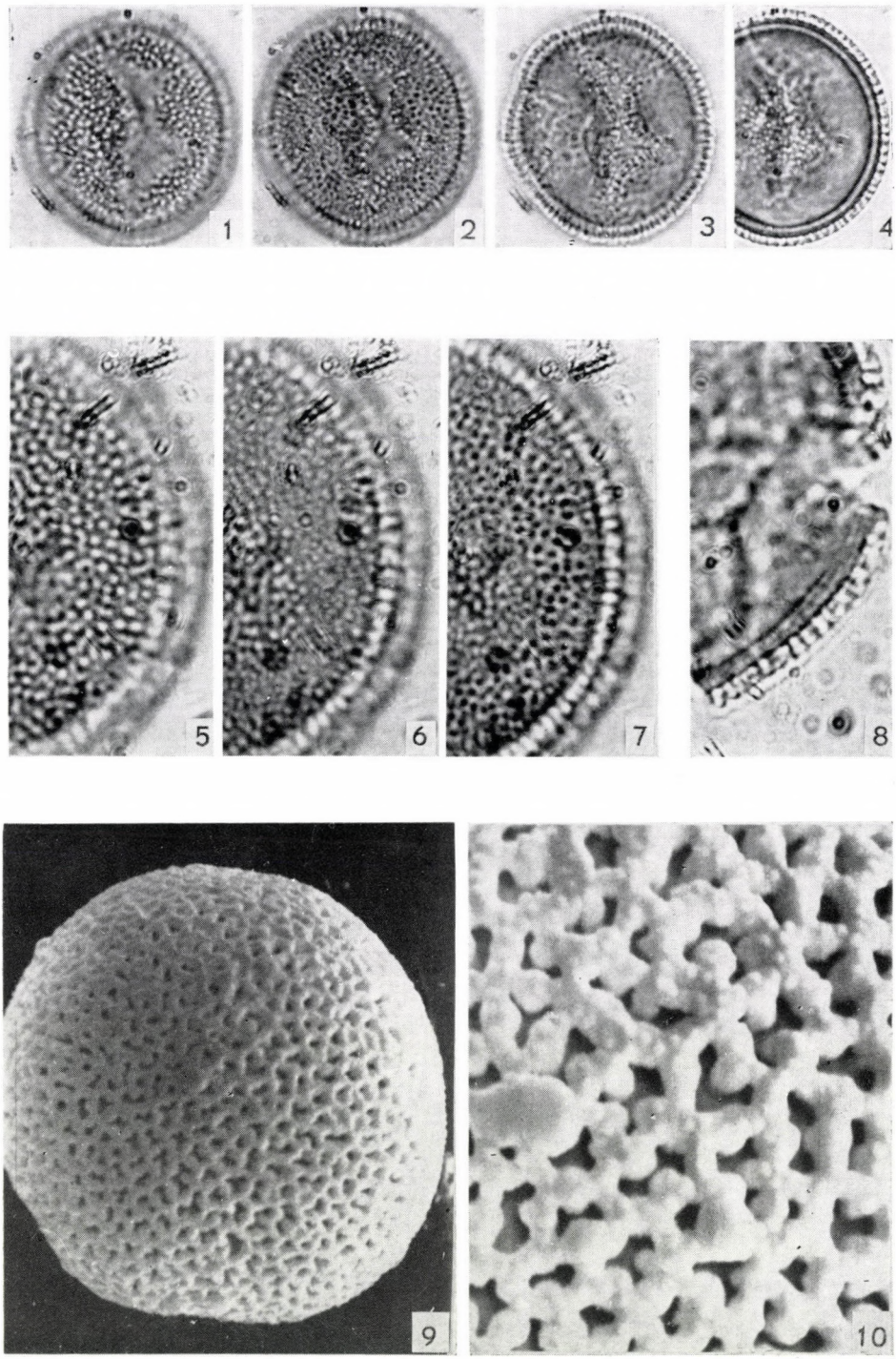


Plate 1

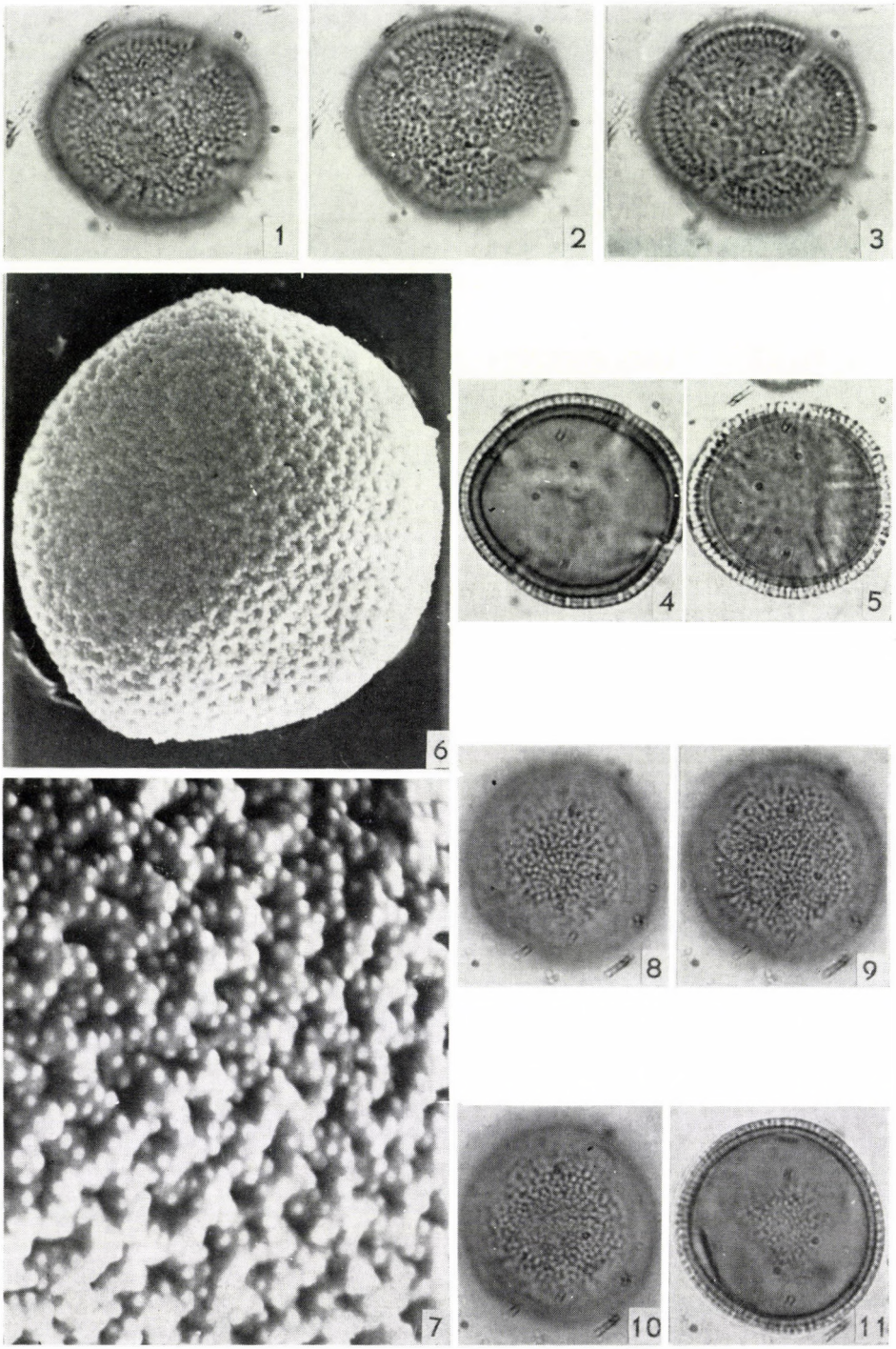
1. Adaxial surface: trichomes, epidermal cells and veins ×90. 2. Abaxial surface: paracytic stomata, trichomes and part of a vein (left-down) ×90. 3. SEM paradermal view of adaxial surface: raised hairs with rounded basis, prominent periclinal walls of epidermal cell ×200, tilt 35. 4. Paradermal view of adaxial surface: single conical hair with rounded base ×1000

cells polygonal in shape with anticlinal walls straight to slightly rounded. With the light microscope triangular thickness were observed at the contact corners of the cells. The periclinal walls of the adaxial surface are prominent as papillae and without ornamentation (Figs 3 and 5). Epidermal cells of the abaxial surface scanty, mainly limited to the subsidiary cells (Figs 2 and 6.) Cells overlying major veins more or less rectangular and arranged in rows (Figs 1 and 2).



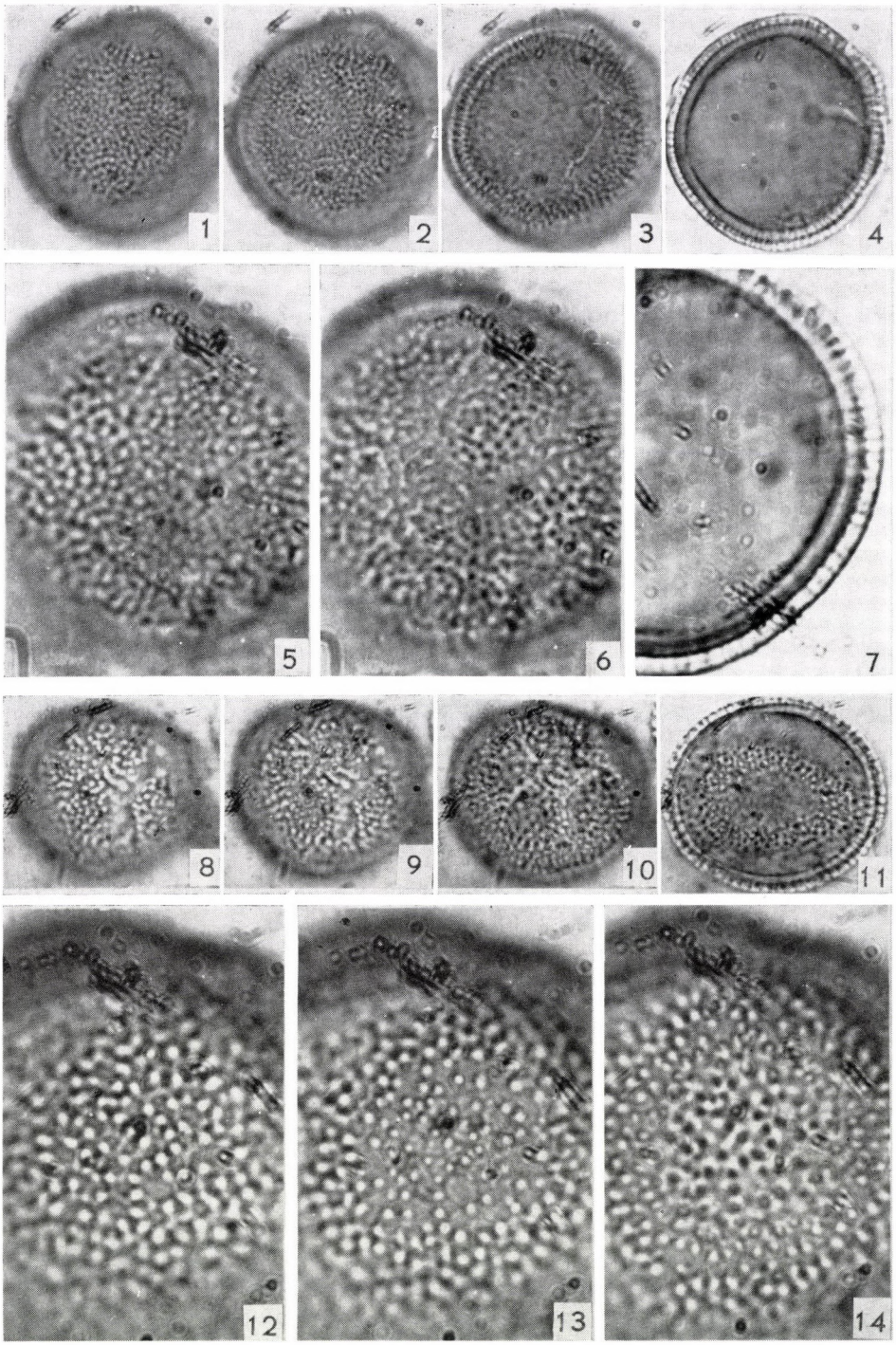
Lamina 1

1–10. *Hedyosmum grisebachii* Solms. 1–4. Granos de polen en diferentes secciones ópticos, ×1000. 5–7. La superficie del grano en diferentes focos ópticos, ×2000. 8. El fragmento del margen del grano, ×2000. 9. SEM, ×3200. 10. El fragmento de la superficie del grano, SEM, ×11 500



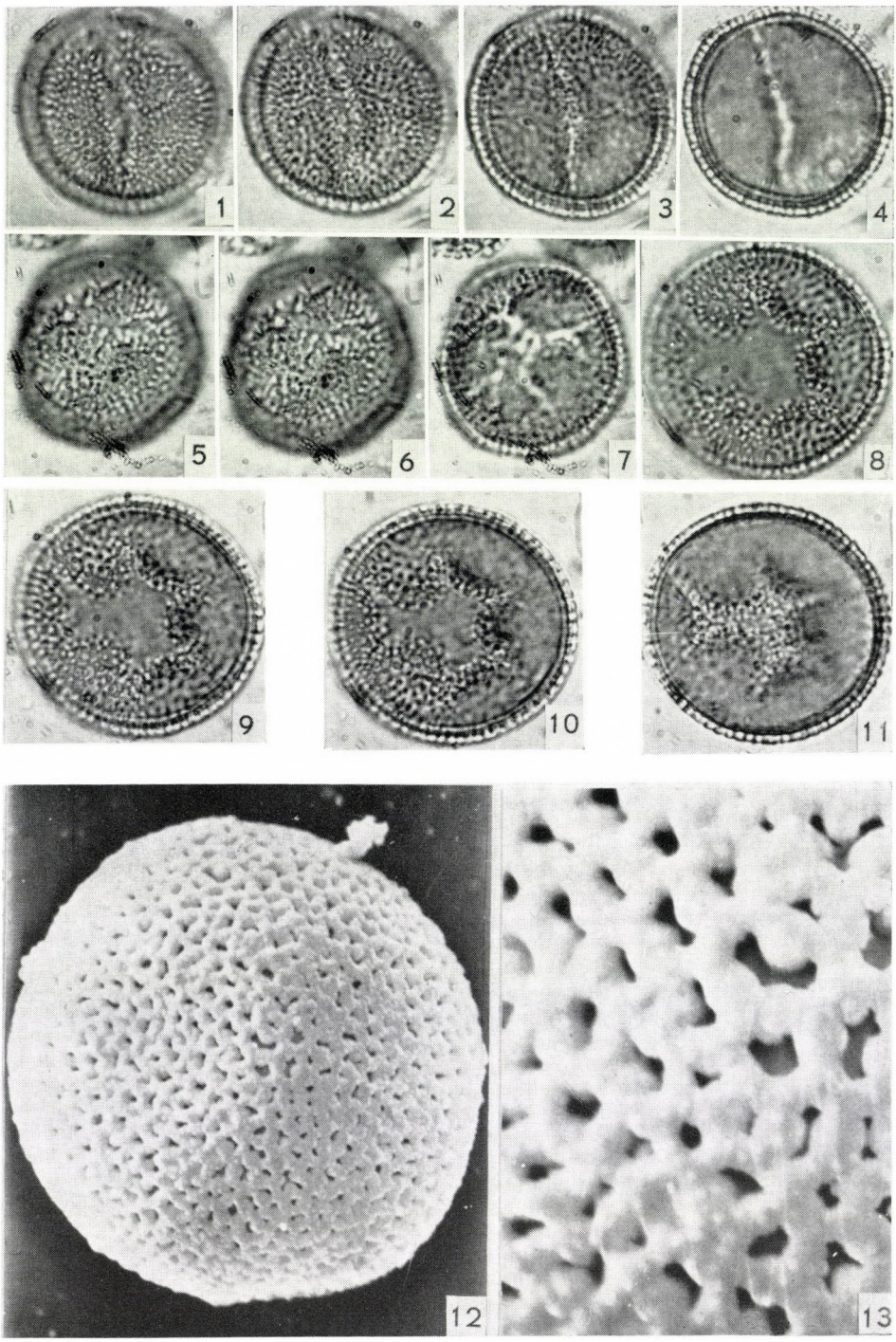
Lamina 2

1–7. *Hedyosmum leonis* Marie Vict. 1–5. Diferentes granos de polen, ×1000. 6. SEM, ×3200. 7. El fragmento de la superficie del grano, SEM, ×11 500. 8–11. *Hedyosmum crassifolium* Urb., ×1000



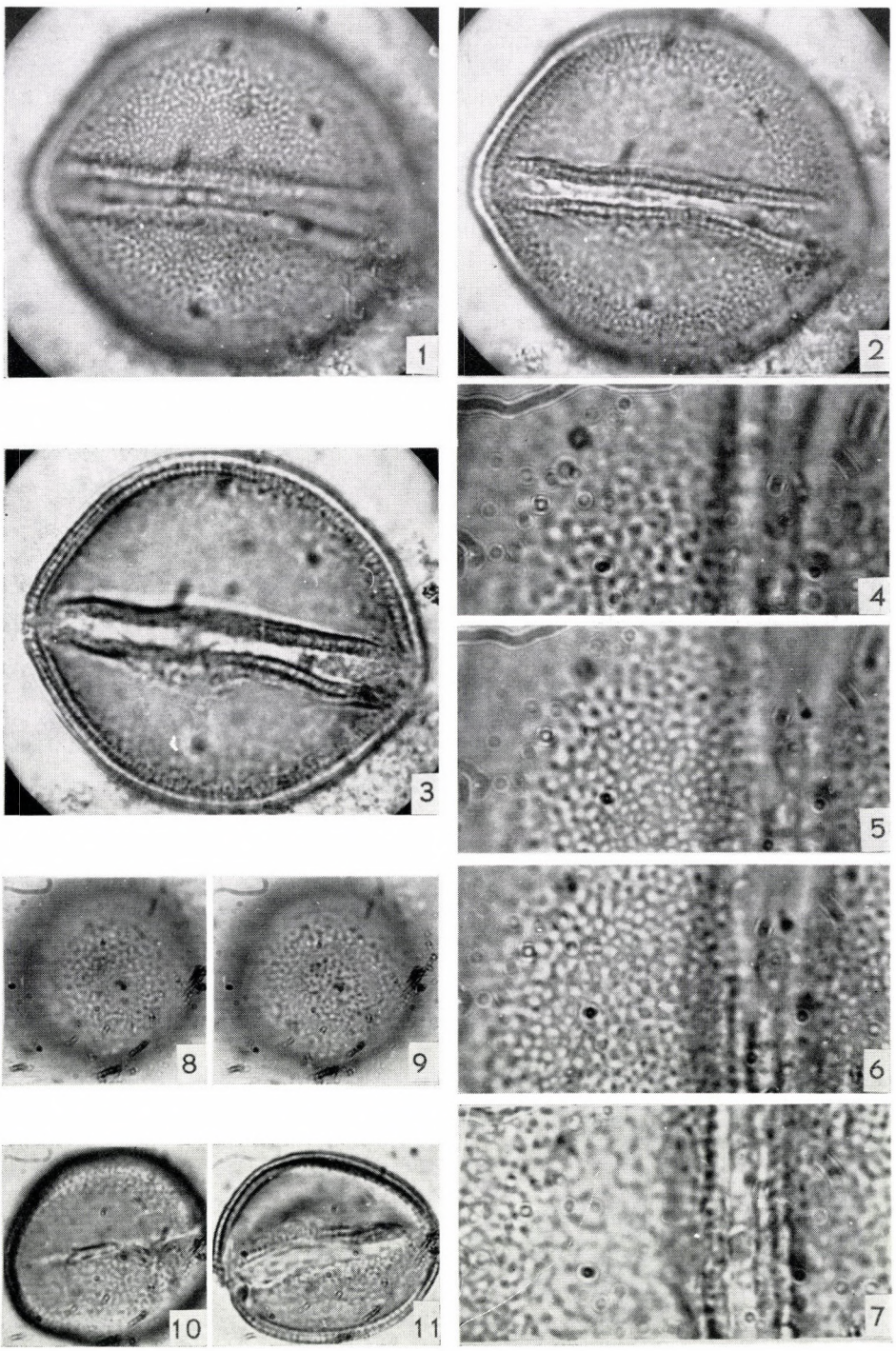
Lamina 3

1–7. *Hedyosmum crassifolium* Urb. 1–4. Granos de polen en diferentes secciones ópticos, ×1000. 5–6. La superficie del grano en diferentes focos ópticos, ×2000. 7. El fragmento del margen del grano, ×2000. 8–14. *Hedyosmum nutans* Sw. 8–11. Granos de polen en diferentes secciones ópticos, ×1000. 12–14. La superficie del grano en diferentes focos ópticos, ×2000



Lamina 4

1–13. *Hedyosmum nutans* Sw. 1–11. Diferentes granos de polen en diferentes secciones ópticos, ×1000. 12. SEM, ×3200. 13. El fragmento de la superficie del grano, SEM, ×11 500



Lamina 5

1–7. *Canella winterana* (L.) Gaertn. 1–3. Grano de polen en diferentes secciones ópticos, ×1000. 4–7. La superficie del grano en diferentes focos ópticos, ×2000. 8–11. *Cinnamodendron cubense* Urb., ×1000

Conclusiones

Todas las especies investigadas del género *Hedyosmum* pertenecen a un solo tipo de grano de polen.

En lo que concierne a las aperturas, se puede ver una transición entre los granos monosulcados hasta polisulcados o colpoidados. La especie *Hedyosmum leonis* tiene los sulcos más divididos que las otras especies, y parece que estas son las transiciones entre los granos sulcados y colpados. ERDTMAN (1969), considera que en la familia Chloranthaceae se encuentran granos de polen intermedios entre sulcados y colpados.

Respecto a la morfología del polen, la familia Chloranthaceae tiene algunas conecciones con otras familias de las Angiospermas primitivas.

De la familia Canellaceae, los géneros *Canella* y *Cinnamodendron*, presentan dos tipos de granos de polen. En el tipo *Cinnamodendron* el grano es más pequeño con la exina más fina y el retículo está menos caracterizado que en el tipo *Canella*.

Por otra parte hay algunas conecciones entre el tipo *Cinnamodendron* y el tipo de polen de la familia Chloranthaceae. Se puede sugerir que el tipo de Chloranthaceae representa un grano desde el punto de vista de la morfología, más antiguo, es decir más primitivo.

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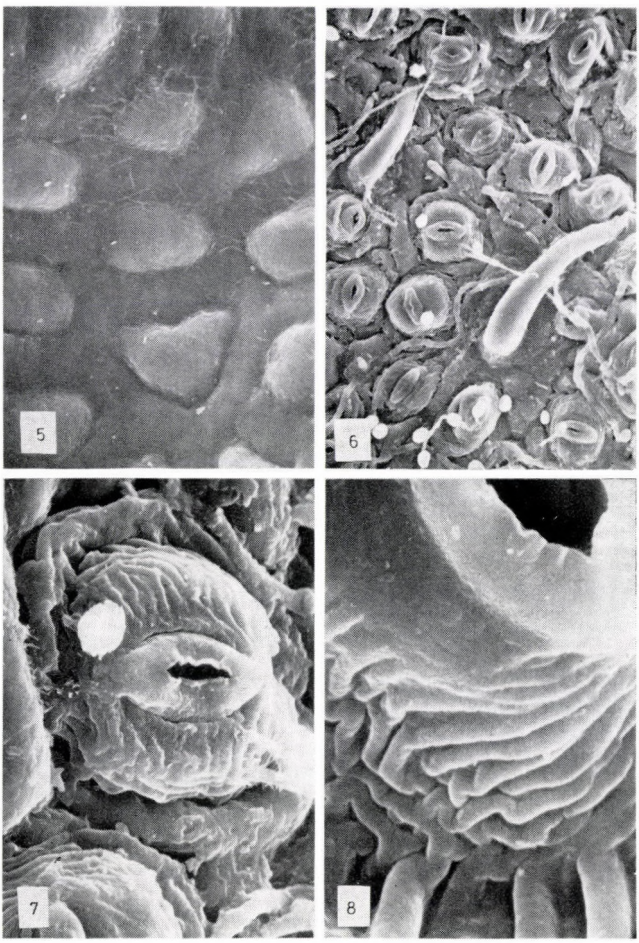

Plate 2

5. Paradermal view of adaxial surface: Prominent periclinal walls of the epidermal cells as little papillae ×1000. 6. Paradermal view of abaxial surface: trichomes, paracytic stomata and wax particles ×500. 7. Paradermal view of abaxial surface: paracytic stomata with ornamentations on the surface of guard-cells ×2000. 8. Paradermal view of abaxial surface ornamentations on the surface of guard-cells and linkage with the subsidiary cells ×5000

Stomata confined exclusively to the abaxial surface, paracytic (Figs 2 and 6). Stomatal complex slightly raised with reference to the epidermal cells; in average 40 μm long and 35 μm wide; guard cells pair 30 μm long and 27 μm wide, the cells elongated reniform in paradermal view, without the so called T pieces at poles, but with fine striations (Figs 7 and 8).

Wax was only observed on abaxial surface as little balls by the scanning electron microscope (Figs 6 and 7).

Material studied: HAC VALES 51, Mogote de la Cueva de Jose Miguel, Viñales 24-11-1974; HAC VALES 362, Viñales, 11-6-1979.

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I wish to express my gratitude to my colleagues at the Department of Botany of the Smithsonian Institution, who prepared the material for the SEM and did all the technical work.

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ESTUDIO TAXONÓMICO DEL GÉNERO *ARIADNE* URB. (RUBIACEAE)*

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(Llegado: 15 Diciembre 1979)

This paper contains a new, more detailed taxonomic revision of the monotypic genus *Ariadne* Urb. (Rubiaceae), endemic to the NE serpentine mountain ranges of Cuba. The genus belongs to the tribe Rondeletieae, as its most evolutioned representative among all Cuban genera. Its generic features and specific and infraspecific units are characterized and discussed. The authors describe as new taxa: *Ariadne shaferi* ssp. *moaensis* ssp. nova, and *Ariadne shaferi* ssp. *moaensis* var. *rivularis* var. nova.

Introducción

Al consultar los distintos tomos de la obra Flora de Cuba (LEÓN y ALAIN 1946–1964) vemos que en general, las descripciones que contiene estan elaboradas hasta nivel de especies, con poca frecuencia presenta taxa infraespecificos; sobre estos y la variabilidad de las distintas especies, se conoce poco.

Actualmente se trabaja en este sentido, para aclarar los problemas que existen en las familias de las plantas que forman parte de la flora de Cuba.

Estudiar la variabilidad y la subordinación sistemática de los géneros y las especies conocidos y comunes en areas determinadas estan importante como reconocer la especies desconocidas en la flora de una región, con el fin de dominar en detalle y con profundidad la flora de un pais.

Con relación a las Rubiáceas, familia de distribución pantropical, con importancia económica, desde el punto de vista industrial, medicinal y alimenticio, es necesario su estudio; en América Tropical no esta explorada por completo y requiere especial atención, además en la flora de Cuba esta familia está reptesentada con mayor numero de especies (79 géneros y alredeor de 500 especies), por ello son importantes las investigaciones taxonómicas y fitogeográficas en este grupo.

Los estudios de las Rubiáceas cubanas, comenzaron en la mitad del siglo XVIII. por JACOUIN, y hasta nuestros dias muchos botanicos destacados; tales como DE CANDOLLE, A. RICHARD, CH. WRIGHT, GRISEBACH, URBAN, STANDLEY y otros dedicaron parte de su actividad cientifica a investigarlas. No obstante, aunque existen resultados valiosos, la exploración de las Rubiáceas cubanas no ha terminado y el material conocido requiere una investigación crítica y multifacetica, no solo en los géneros de gran variabilidad, como *Rondeletia* L., *Psychotria* L. y *Guettarda* L., sino también en los géneros monotipicos endémicos, como lo es *Ariadne* Urb. del Norte de Cuba oriental.

* Rubiáceas Cubanas V.

Material and métodos

Con el fin de estudiar la variabilidad morfológica de este género, despues de observar que la forma y tamaño de las hojas y el tamaño de los frutos eran los caracteres sobresalientes, se hizo un análisis de variabilidad de hojas y frutos en relación con factores ecológicos y con la distribución geográfica de las poblaciones de la especie, para determinar el grado de variación taxonómica entre los ejemplares estudiados. En ejemplares de la especie *Ariadne shaferi* de los herbarios del HAC, HAJB, BM, K, F, MBG, GOET, NY, S, US, asi como los ejemplares colectados por el colectivo de trabajo, se midió largo y ancho de las hojas, largo de los frutos, del pecíolo, angulo a partir del nervio lateral del nervio medio; se confeccionaron gráficos de largo/ancho de las hojas y largo de fruto por la relación largo/ancho de hojas, y mapa de distribución de las poblaciones investigadas.

Además de lo antes mencionado se estudiaron todas las caracteristicas morfológicas y estructurales para controlar y completar las descripciones anteriores que se hicieron para el género y especie.

Descripción de los taxa

ARIADNE Urban, Feddes Repert. XVIII: 25, 1922.

Arbustos o arbolitos, ramitas cuadrangulares; estipulas triangulares, agudas, no connadas; hojas elípticas aovadas, oblongo-ovales, suborbiculares a orbicular-obovadas, cartáceas o subcoriaceas. Inflorescencias axilares, cimosas, flores 4-meras; tubo del caliz obovado-oblongo, truncado, limbo cupulifero, lóbulos desiguales por pares; tubo de la corola mas corto que los lóbulos, lóbulos imbricados; estambres adnatos en la garganta de la corola en la parte superior del tubo; anteras mayormente elípticas a oblongo-obovadas, dorsífijas y sésiles en la

Fig. 1. Isotipo de *Neomazaea shaferi* Standl. in HAC; SHAFER 3313

garganta de la corola; estilo ensanchado, capituliforme, ligeramente bilobulado, estigma orbicular. Ovario bilocular, lateralmente comprimido, pubérulo en la parte superior, disco anular estrecho; ovulos 2, raramente 1 por celda; cápsula oblonga u obovado-oblonga, lateralmente muy comprimida, pericarpio crustáceo, que abre primero en forma septicida, endocarpio córneo u óseo con dehiscencia loculicida posterior. Placenta linear, unida al septo sobre la base en forma peltada, libre arriba, extendiendose hasta la mitad de la cápsula; semillas verticales, peltadas, lanceo-lineares, triangulares en sección transversal, sin alas laterales, semisuperpuestas con su superficie dorsal fijadas a la mitad de la placenta en forma peltada.

Situación taxonómica del género

La especie típica del género fue descrita por STANDLEY (1918) como miembro del género *Neomazaea* (*N. shaferi*). URBAN (1922: 25) cuando describió el género *Ariadne* consideró ubicarlo en la cercania del género *Phyllomelia* de la tribú Ixoreae. Posteriormente cambió de opinión y situó el género después de *Neomazaea* dentro de la tribú Rondeletieae (1923: 148–149), y puntualizó las diferencias esenciales entre los dos géneros.

Neomazaea Kr. et Urb. difiere de *Ariadne* Urb. en tener lóbulos del cáliz iguales, deciduos después del periodo de floración y fructificación, tubo de la corola alargado, filamentos evolucionados, anteras lineales, estilo marcadamente bilobulado, óvulos 4–6 por celda; cápsula cuadrangular, no comprimida, que se abre en forma septicida, placenta lineal, fijada en toda su longitud al septo.

Al comparar los caracteres de los géneros cubanos que pertenecen a la tribú Rondeletieae, encontramos que algunos de ellos mas evolucionados estan presentes en el género *Ariadne*, como son: la simetria bilateral que tiene el caliz y ovario, el bajo numero de óvulos y semillas por celdas, el tipo de inserción de la placenta que posee. Es por ello que consideramos que el género *Ariadne* como el mas evolucionado de los géneros cubanos dentro de la tribú.

Ariadne shaferi (Standl.) Urban in Symb. Ant. 9: 148 (1923)

Typus: SHAFER 3313, Prov. Holguin (Oriente), Sierra de Nipe, entre el camino de Piedra Gorda a Woodfred. 28. 12. 1909. NY. Isotypi: HAC, GH, US.
Basónimo: *Neomazaea shaferi* Standley in North Amer. Fl. 32: 42 (1918).
Sinónimo: *Ariadne ekmanii* Urban in Feddes Repert. XVIII: 26. (1922); *Pisonia inermis* Griseb. Catal. Pl. Cub. 1866: 24 p.p. non Jacq.

Arbustos o arbolitos, mayormente 2–3 m; estípulas de 1–2 mm, triangulares, agudas, no connadas, persistentes; hojas elípticas-aovadas, oblongo-ovales, suborbiculares a orbicular-obovadas de 3–5,5–(7) por 1,5–4–(5) cm, redondeadas aguditas a menudo diminutamente apiculadas en el ápice, estrechadas hacia el pecíolo en la base, cartáceas o subcoriáceas, los renuevos rojizos; margen plano o subrevoluto; nerviación aparente en ambas caras. Inflorescencia de 1–1,5 cm, en cimas axilares 3-floras, pedicelos de 0,3–0,8 mm, flores 4-meras; tubo del cáliz obovado-oblongo, truncado, algo ondulado, de 1–1,5 mm; lóbulos oval-obovados, corola pequeña de 2–3 mm, tubo de la corola de 0,5–0,8 mm de largo, lóbulos de la corola desiguales por pares, 2 ovales de 2 mm de largo y ancho y 2 anchamente aovados a semiorbiculares de 3 mm de largo y ancho; estambres de 1–1,2 mm, adnatos en la garganta de la corola, filamentos de 0,8–0,9 mm de largo, estilo de hasta 3 mm de largo; ovario 2-locular de 2,5–3 mm de largo; cápsula oblonga u obovado-oblonga, comprimida lateralmente de 0,5–1,8–(2) cm de largo. Semillas 2 por celda, verticales, peltadas, sin alas laterales.

Clave para los taxa infraespecificos:

1 a Fruto de hasta 1 cm de largo, hojas elípticas o aovadas de 3–5 cm de largo ..... 1. ssp. *shaferi*

b Fruto de 1–1,8 cm de largo, hojas suborbiculares u orbicular-obovadas, o cuando elípticas, entonces mayores ..... 2. ssp. *moaensis*

— hojas suborbiculares u orbicular-obovadas, frutos de 1–1,5 cm de largo ..... 2a var. *moaensis*

— hojas elípticas u oblongo-elípticas de hasta 7 cm de largo; fruto hasta 2 cm ..... 2b var. *rivularis*

1. **Ariadne shaferi** (Standl.) Urb. **ssp. shaferi**

Hojas elípticas a aovadas, de 3–5 cm de largo por 1,5–3,5 cm de ancho. R largo/ancho mayor de 1,5. Fruto loculicida de hasta 1 cm de largo.

Area: Cuba; Prov. Holguin: Sierras de Nipe y Cristal, endémica.

Ejemplares examinados: SHAFER 3313 Prov. Holguin, Sierra de Nipe, entre el camino de Piedra Gorda a Woodfred. Formación de serpentina, 400–500 m de alt. 28. 12. 1909. (Holotipo e isotipos) — EKMAN 15884 Prov. Holguin, Sierra del Cristal 12. 1922 — WRIGHT 2729; — UO 1005; Prov. Holguin Pinares de Mayari, Loma la Cinturita, LOPEZ FIGUEIRAS 27–31. 5. 1960. — L. F. 2805 Prov. Holguin, Pinar Colorado, Cayo Rey, Sierra de Nipe 2. 9. 1956. — LS 4070 Prov. Holguin Sierra de Nipe, Mayari, J. P. CARABIA Mayo, 1940. — L. F. 2859 Prov. Holguin, Charrascales del Pinar Colorado Cayo Rey, Sierra de Nipe; 27. 4. 1957. ACUÑA 11909; Prov. Holguin Falda N de Sierra de Nipe, C. W. MORTON y ACUÑA, 15. 10. 1941. — L. F. 1723 Prov. Holguin, charrascales de la cantera Finca La Caridad, Sierra de Nipe, 26. 11. 1954. — LS 4057, Prov. Holguin Pinares de Sierra de Nipe, Mayari, J. P. CARABIA, Mayo. 1940. — LS 4585 Prov. Holguin charrascales de Sierra de Nipe, Mayari J. P. CARABIA, Mayo 1940. — HAC 27911 Prov. Holguin Sierra de Nipe, Pinares de Mayari, BORHIDI y MUÑIZ 18. 7. 1970; — HAC 27912 Idem. — UO 2059 Prov. Holguin, Pinares de Mayari, La Bandera, Sierra de Nipe, LÓPEZ FIGUEIRAS 27–31. 5. 1960. — ACUÑA 24670 Prov. Holguin, Sierra de Saca la Lengua, Sierra del Cristal, Mayari Arriba; ACUÑA y ZAYAS 26–27. 5. 1955. — 30744 HAJB Idem, BISSE, L. GONZALEZ, J. GUTIERREZ, A. ARECES, y MANITZ, — 28416, 28417, 28418, 28419, 28420, 28421, 28422, 28423, 28424, 28425 HAC Prov. Holguin Loma La Bandera, Mayari Sierra de Nipe, M. FERNANDEZ, P. HERRERA, I. GRUDZINSKAYA, M. I. TORRES, 19. 5. 1978.

2. **Ariadne shaferi** (Standl.) Urb. **ssp. moaensis** Fernandez et Borhidi **ssp. nova**

A typo differt: foliis ovato-suborbicularibus vel orbiculari-obovatis vel rariter oblongo-ovalibus, dimensione variis usque ad 7 cm longis; relatione (R) longitudo-latitudine variabilibus, fructibus majoribus 1–1,8–(2) cm longis.

Difiere del tipo en tener hojas aovadas, suborbiculares a orbicular-obovadas y oblongo-ovales de tamaño variable hasta 7 cm de largo; R (longitud/latitud de las hojas) es variable. Fruto mayor y llega tener 1,8(2) cm de largo.

Area: Cuba; Provincias Holguin y Guantánamo; Sierras de Moa y Toa; endémica.

Dentro de esta subespecie distinguimos 2 variedades, segun la ecología del lugar donde se desarrolan, que son:

Fig. 2. Ejemplar representativo del *Ariadne shaferi* ssp. *moaensis* Fernandez et Borhidi **var.** *moaensis* en HAC; CLEMENTE 7423

var. moaensis:

foliis suborbicularibus vel orbiculari-obovatis, relatione longitudo/latitudine **minore** quam 1,5; fructis 1–1,5 cm longis.

Holotypus: CLEMENTE 6223 HAC; Cuba Prov. Holguin; Cerro de **Cananova**, Moa; col.: CLEMENTE, NESTOR y CRISÓGONE 1948.

var. moaensis:

hojas suborbiculares a orbicular-obovadas; R es menor de 1,5; fruto de hasta **1,5 cm** de largo.

Habitat: Crestas y pendientes secas, en charrascales y pinares abiertos sobre **latosoles** de serpentina.

Fig. 3. Holotipo del *Ariadne shaferi* ssp. *moaensis* var. *rivularis* Fernandez et Borhidi en HAC León 20154

Ejemplares examinados: 27909 y 27910 HAC; Prov. Holguin, Charrascos del Rio Yamaniguey, Región de Moa, col.: Borhidi, Muñiz y Vazouez 23. 3. 1970. — L. F. 1227; Prov. Holguin; charrascales Cerro de Miraflores, Cananova, 15–16. 4. 1954. — Alain 3362; Prov. Holguin; charrascos Sierra de Moa, 800 m de alt. 25–26. 7. 1953. — Alain 939 (Clemente 6839); Prov. Holguin, Pinares de Moa cerca del Rio Yagrumaje 7. 1949. — Clemente 4384 Prov. Holguin; bosques al E del Aeropuerto de Moa; 26. 6. 1945. LS 1276 Prov. Holguin; Cerro de Miraflores, Cananova, charrascos de serpentina; López Figueiras 15–16. 4. 1954. — Clemente 4384 (3599 en LS), Prov. Holguin; bosque al E. del aeropuerto de Moa; 5. 1944. — Acuña 12738; Prov. Holguin Playa de la Vaca, Moa, 11. 4. 1945. — Mrs. Bucher 25; Roig 8206; Prov. Holguin, Moa; 9. 1939. — Clemente 3549 (3537 LS) Prov. Holguin, Moa, Pantano al E. de Campo de Aviación; 5. 1944. — León 20121; Prov. Holguin, Llano humedo del Aeropuerto, Moa. col.: León, Clemente y R. A. Howard; 21. 7. 1941. — Clemente 7403; Prov. Holguin, Camino del Centeno al Cerro de Cananova; col.: Clemente, Nestor y Crisógone; 8. 1950. — León 20277; Prov. Holguin; Manigua cerca de Playa de Moa; col.: León, Clemente y R. A. Howard, 25. 7. 1941. — LS 21802; Prov. Holguin; Playa de Moa; col.: Marie-Victorin, Clemente y Alain; 4. 1943. — Acuña 27057; Yamaniguey, Moa; charrasco serpentinoso; col.: grupo Samek; 20. 2. 1968. — Clemente 3596; Prov. Holguin, Bosque al E del Aeropuerto, Moa; 15. 5. 1944. — HAC 27515; Prov. Holguin, Moa, Mina la

Melba; col.: E. Del Risco y otros; 31. 3. 1972. — León 21123; Prov. Holguin, Moa; Cerro de Miraflores, Cananova, 7. 1942; — Clemente 3587; Prov. Holguin, Moa, pantano al O. del Campo de Aviación; 5. 1944. — León 20129; Prov. Holguin; Llano humedo cerca de la pista de aterrizaje, Moa; col.: León, Clemente y R. A. Howard; 21. 7. 1941.

var. rivularis Fernandez et Borhidi **var. nova**

A varietate typica differt foliis majoribus, usque ad 7 cm longis, oblongo-ovatis, relatione longitudo/latitudine foliorum 2–2,5; fructibus usque ad 2 cm longis.

Holotypus: León 20154; HAC; Prov. Holguin; Pinares de Moa, cerca de Arroyo Jicotea; col.: León, Clemente y R. A. Howard; 22. 7. 1941. Isotype: A, US.

var. rivularis Fernandez y Borhidi **var. nova**

Difiere de la variedad típica en tener hojas oblongo-ovales, mas grandes que los demás taxa de esta especie, el largo de las hojas llega hasta 7 cm; R: 2–2,5; el tamaño del fruto alcanza hasta 2 cm.

Habitat: Lugares humedos en orillas de arroyos, en bosques siempreverdes humedos de serpentina.

Ejemplares examinados: 14662 HAC; Cuba, Oriente, Levisa; Sierra del Cristal; col.: van Hermann 10. 1943. — Clemente 3625; Prov. Holguin, Moa, Rio Yamanigüey, 5. 1944. — Alain 5840; Prov. Holguin, Charrascos del Rio Miguel, Sierra del Cristal; col.: Alain, Acuña y López Figueiras; 2–7. 4. 1955. — Alain 3433; Prov. Holguin; Charrascos Sierra de Moa en 800 m de alt.; 25–26. 7. 1953. — Clemente 3858; Prov. Holguin Rio Yagrumaje del Medio, Punta Gorda; col.: Clemente, Alain y Crisógone; 18. 7. 1944. — 28427 y 28428 HAC; Prov. Holguin, Desembocadura del Rio Yamanigüey, Moa; col.: Borhidi, Muñiz y Vazouez, 24. 3. 1970. — 5935 Howard; Oriente, Sierra de Moa, foothills on pine wooded hillside; 7. 1941.

Hay que considerar, que además de los taxa mencionados tenemos algunas colectas de la zona de serpentina de Baracoa, estos ejemplares muestran una tendencia a tener hojas coriáceas, con una nerviación marcada y una variabilidad grande en cuanto a la forma y tamaño de las hojas, pero son escasos y estériles. Ejemplar representativo con flores y frutos no se ha localizado. Todo el material proviene de charrascal de La Cuaba, cerca de Baracoa. Hay probabilidad, que estas poblaciones pueden formar una segunda especie de este género monotipico cubano.

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A PRELIMINARY NUMERICAL TAXONOMIC STUDY OF THE *SCILLA BIFOLIA* AGGREGATE (LILIACEAE, SCILLOIDEAE) IN HUNGARY

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Fifteen morphological and two phenological characters were recorded in twenty-six populations of the *Scilla bifolia* aggregate grown under uniform conditions. Two multivariate techniques, sum of squares clustering and principal component analysis, were used to study the variation among populations. Both methods revealed three distinct groups, suggesting the existence of three species in Hungary. These are recognized as *S. vindobonensis*, *S. kladnii* and *S. buekkensis*, all described earlier. A fourth group may also be distinguished at a lower level, its taxonomic position remains doubtful, however.

Introduction

The geographic variation of *Scilla bifolia* L. populations in Hungary has been the subject of recent surveys applying traditional taxonomic techniques (cf. KERESZTY 1983). The authors' observations and reports from neighbouring countries (SPETA 1974, 1977) suggest that *Scilla bifolia* is a group, including a number of more or less distinct forms, rather than a single species. However, proposals to create a new taxonomy of this complex have not yet been justified by the use of numerical techniques. The present paper is therefore an attempt to meet a long need by providing cluster analysis and ordination results. Although this study is based on populations only from Hungary, it is expected that the results will be informative and useful to an overall revision of this species complex. Since *S. bifolia* is a protected species in Hungary, the findings may also have relevance to plant conservation.

Material and methods

A collection of twenty-six population samples from thirteen different geographic regions of Hungary was assembled. The geographic localization of sampling sites is shown by the map in Fig. 1. The regions and collecting localities are listed in Table 1, together with phytosociological and phytogeographical data. The nomenclature follows Soó (1964) for syntaxa, and PÓCS (1968) for phytogeographical units. The code numbers refer to the grid system used by the Central European flora mapping project (cf. EHRENDORFER 1973). In order to obtain reliable data to indicate genetic differences and similarities, the sample individuals were grown under uniform environmental conditions in the garden of the Research Institute for Botany, Vácrátót, in 1979–1980. All plants were cultivated for at least two years before measurements were taken in 1982.

Fifteen morphological and two phenological characters were selected for the study. The morphological characters were measured and recorded for ten plant individuals (OTUs) from each population at the time of full flowering, i.e., when all flowers were open. If the number of flowers per inflorescence was over six, the uppermost flower was allowed to be in bud and/or the lowermost to be ceased. Eight characters are continuous, nine are determined

Table 1

List of regions and collecting sites of Scilla bifolia populations used in this study

Geographic region	Phytogeographic region and district	Locality	Code No.	Plant community	Altitude, m	Date
I. Danube Basin, upper floodplain	Eupannonicum–Arrabonicum	1. Győr, Püspökerdő	8371		100	8. 5. 1979
		2. Zsejkepuszta	8271			
		3. Vámosszabadi, Határerdő	8272			
II. Danube Basin, middle floodplain	Eupannonicum–Praematricum	4. Kisoroszi	8180	*Fraxino pannonicae–Nlmetum*	80	4. 5. 1979
	Eupannonicum Colocense	5. Ráckeve, Angyali sziget	8779			30. 4. 1979
		6. Makád, Csepel sziget	8979			4. 5. 1979
III. The foothills of Bakony Mts	Bakonyicum–Veszprémiense	7. Bakonypölöske, Kupi erdő	8770	*Aegopodio–Alnetum quercetosum*	200	12. 4. 1979
		8. Pápakovácsi, Gannai erdő	8771			
IV. Velencei Mts		9. Nadap, Templom hegy	8777	*Aceri tatarico–Quercetum ornetosum*	240	10. 4. 1979
V. Börzsöny Mts	Matricum–Neogradense	10. Nagyhideghegy, top	8079	*Aconito–Fagetum*	850	27. 4. 1979
		11. Nagyhideghegy, eastern slope				
VI. Bükk Mts	Matricum–Borsodense	12. Cserépfalu, Hór völgye	8089	*Fagetum silvaticae*	260	6. 5. 1979
		13. Felsőtárkány, Várhegy	8088	*Querco–Fagetum*	650	20. 4. 1979
		14. Répáshuta, Kerekhegy	8089	*Tilio–Fraxinetum*	650	27. 4. 1979
VII. Zempléni Mts	Matricum–Tokajense	15. Makkoshotyka, Völgypatak valley	7695	*Aegopodio–Alnetum*	350	10. 5. 1979

	Carpaticum–Cassovicum	16. Füzérradvány, Vilypuszta	7595	*Querco petreae–Carpinetum*	280	
VIII. Hortobágy Nat. Park, Great Hungarian Plain	Eupannonicum–Crisicum	17. Újszentmargita, Margitai erdő	8292	*Galatello–Quercetum*	100	25. 4. 1979
IX. Western Transdanubia	Praenoricum–Castriferreicum	18. Ikervár, erdő	8767	*Querco–Ulmetum*	150	12. 4. 1979
		19. Ikervár, rét				
X. Tolna County	Praeillyricum–Kaposense	20. Pálfa, Simontornyai erdő	9277	*Helleboro dumetorum–Carpinetum*	230	30. 3. 1979
XI. Mecsek Mts	Praeillyricum–Sopianicum	21. Égervölgy	9875	*Helleboro odoro–Fagetum*	230	10. 4. 1979
		22. Pécs, Tubes		*Tilio argenteae–Fraxinetum*	500	11. 4. 1980
XII. Villányi Mts	Praeillyricum–Villányicum	23. Szárszomlyó, at Nagyharsány	9875		300	10. 4. 1980
		24. Ördögvölgy		*Asperulo taurinae–Carpinetum*	200	
XIII. Békés County, Great Hungarian Plain	Eupannonicum–Crisicum	25. Doboz, Fenyeresi erdő	9293	*Querco–Ulmetum*	120	29. 4. 1979
		26. Vargahossza erdő			100	

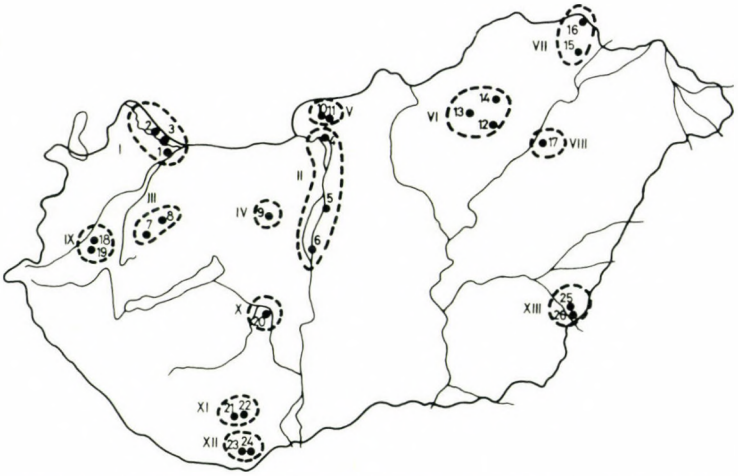

Fig. 1. The geographic localization of *Scilla bifolia* populations used in this study. See Table 1 for explanation of numbering

by binary codes. The continuous characters include three dimensionless ratios. The characters and character states, where applicable, are listed below together with the abbreviations used in the figures:

1. L: "leaf ratio" (length/width)
2. I: "inflorescence ratio" (stem length/length of main inflorescence axis)
3. N: number of leaves
4. P: number of pedicels
5. F: "flower ratio" (tepal length/filament length)
6. S: number of seeds per fruit
7. M: length of mature seeds
8. C: chromosome number
9. E: elaisome shape; 0: variable, surface is grained, 1: cylindrical and smooth
10. G: stem colour; 0: green, 1: reddish
11. R: root thickness; 0: thick, 1: thin
12. B: stem bud colour; 0: bluish-grey, 1: green
13. T: tepal colour; 0: white spotted, 1: blue
14. U: premature fruit colour; 0: reddish, 1: green
15. D: dry seed colour; 0: light ochre, 1: dark brown
16. X: date of complete leaf marcescence; 0: before 25 May, 1: after 25 May
17. Y: first day of flowering; 0: before 31 March, 1: after 31 March

The measurements were summarized in a 260×17 raw data matrix. The means for each character formed another input matrix to analyze relationships among populations coming from thirteen geographic regions of Hungary.

Two multivariate techniques were used to reveal group structure of populations which can be contrasted with the taxonomic considerations. First, an R-type principal component analysis (Seal 1964) was performed using program PRINCOMP (Podani 1984). The resulting ordination depicts potential groupings and/or continuous variation in the data. The component correlations obtained indicate which characters are associated with each axe of variation. The correlation matrix was scrutinized to find positively and negatively characters for future use in taxonomic descriptions. Secondly, the set of populations from thirteen regions (see Table 1) was subjected to sum of squares agglomeration clustering (cf. Orlóci 1978) based on normalized character means. The cluster analysis was performed by program NCLAS

from the SYN-TAX package (PODANI 1980, 1984). The resulting classification was then compared to the groups depicted by the ordination. All computations were done on the IBM 3031 computer of the Hungarian Academy of Sciences.

Results

Character correlations

The entire correlation matrix of characters is not presented. Instead, correlation coefficients exceeding the arbitrary level of 0.6 are listed in Table 2. It is seen that three variables, namely chromosome number (C), elaisome shape (E), and the date of complete leaf marcescence (X), occur most frequently in the table. Chromosome number is strongly correlated with both phenological characters and the colour of stem buds, tepals and dry seeds. Also, as the largest negative coefficient indicates, large chromosome number is probably associated with relatively short mature seeds. The observation that the coefficients between E and other five binary variables are negative is simply the matter of coding.

Table 2

Correlation coefficients exceeding the arbitrary level of |0.6|
See text for character symbols

Characters	Correlation	Characters	Correlation
N — C	0.976	M — C	—0.974
N — P	0.95	E — B	—0.857
X — B	0.854	E — U	—0.857
X — T	0.854	E — T	—0.857
X — D	0.854	E — D	—0.857
Y — D	0.854	E — X	—0.731
Y — B	0.854	E — Y	—0.731
X — C	0.843	G — P	—0.713
Y — C	0.843	G — L	—0.694
L — M	0.831	S — F	—0.657
S — B	0.742	G — N	—0.642
D — S	0.742	E — C	—0.617
C — B	0.72	L — F	—0.61
C — T	0.72		
C — D	0.72		
U — B	0.69		
U — T	0.69		
U — D	0.69		
Y — X	0.675		
C — N	0.675		
S — X	0.653		
M — X	0.647		
S — R	0.614		

Leaf ratio and seed length are positively correlated. The results suggest that increase in the number of leaves (i.e., three leaves instead of two) implies an increase in the number of pedicels. These changes are apparent consequences of an increased chromosome number (36 or 54, instead of the diploid 2n = 18).

Component correlations

The first three components extracted from the correlation matrix explain a total of 70% of the variance. The first component accounts for 48%, which is an unusually high percentage. The second and third components explain 13% and 8%, respectively. The coefficients for the first three eigenvectors associated with the first three eigenvalues are illustrated in Figs 2–3. As seen, the following characters had strong influences on the components: on PCl, three quantitative characters (chromosome number, number of seeds per fruit, and the length of mature seeds) and six binary characters (elaisome shape, dry seed colour, stem bud colour, tepal colour, first day of flowering, date of complete leaf marcescence, and premature fruit colour); on PC2, number of leaves and the flower ratio; and on PC3, stem colour. That is, there is no character highly correlated with more than one of the first three components. Leaf ratio, inflorescence ratio, the number of pedicels, the length of mature seeds and root thickness are not strongly associated with any of these components, although these characters have some outstandingly high correlations with others (cf. Table 2).

Ordination and classification

The ordination of sample individuals is shown in Figs 4–5. For clarity, the positions of OTUs are not indicated in the scattergram. Instead, each group of individuals collected within the same region is outlined in the ordination space. Note that most of these groups contain more than one population (cf. Table 1).

The bipolar first component makes a clear distinction between two groups. Large negative scores are assigned to populations coming from a variety of regions: the upper and middle floodplains of the Danube (I–II), the foothills of Bakony Mountains (III), Mecsek Mountains (XI), Villányi Mountains (XII) and Békés county, Great Hungarian Plain (XIII). These populations do not overlap completely, there is a slight separation between I and XI, and all others if the components are simultaneously examined.

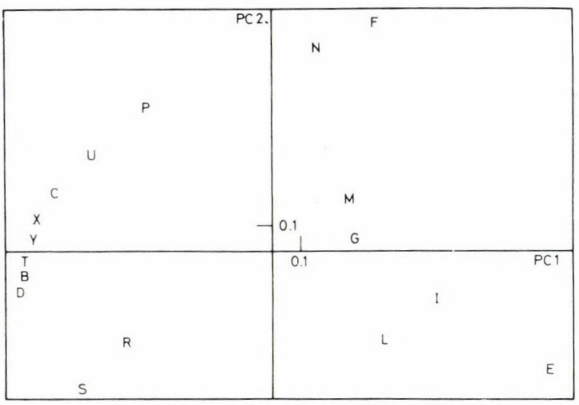

Fig. 2. The correlations of characters with PC1 and PC2. See text for explanations of symbols

The group on the positive end of PC1 includes populations from hilly and mountainous areas, with one exception (Hortobágy National Park). The second and third components reveal the fine structure of this group. The populations from Zemplén (VII) are separated from the others on PC2, and those from western Transdanubia (IX) on PC3. On the fourth component the populations overlap one another, therefore it is not illustrated.

The classification of populations (Fig. 6) is in a very good agreement with the ordination. At two group level, the classification equals to the partition revealed on PC1. Within

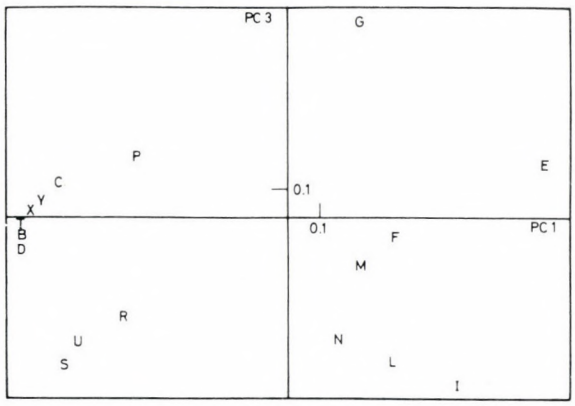

Fig. 3. The correlations of characters with PC1 and PC3. See text for explanations of symbols

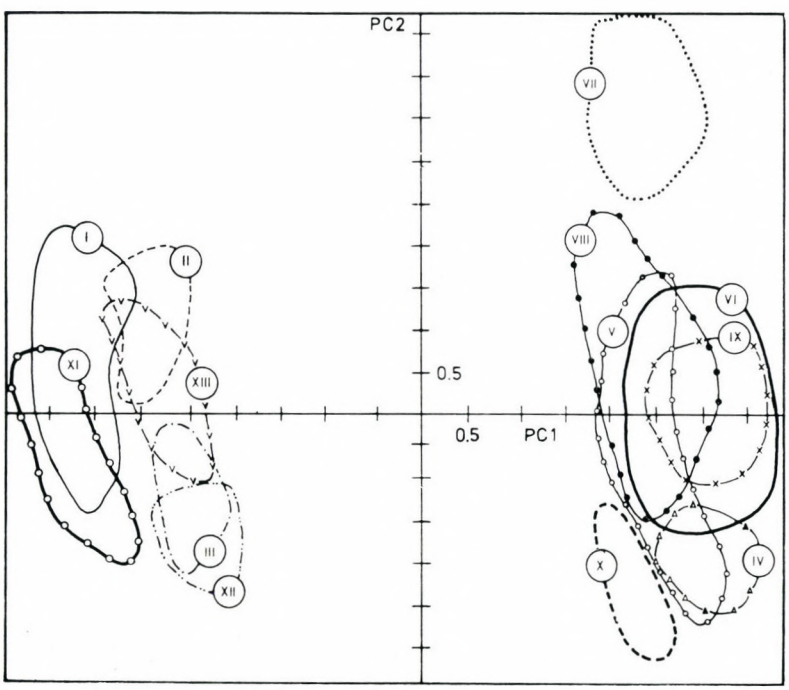

Fig. 4. Principal components ordination of populations on the first two components. See Table 1 for numbers

western Transdanubia are separated from the others. The close relationship between I and IX is also seen in the dendrogram. However, the hierarchy does not suggest their segregation from II, III, XII and XIII, contrary to the PCA results.

the larger group first the populations from the Zemplén Mountains, and then those from

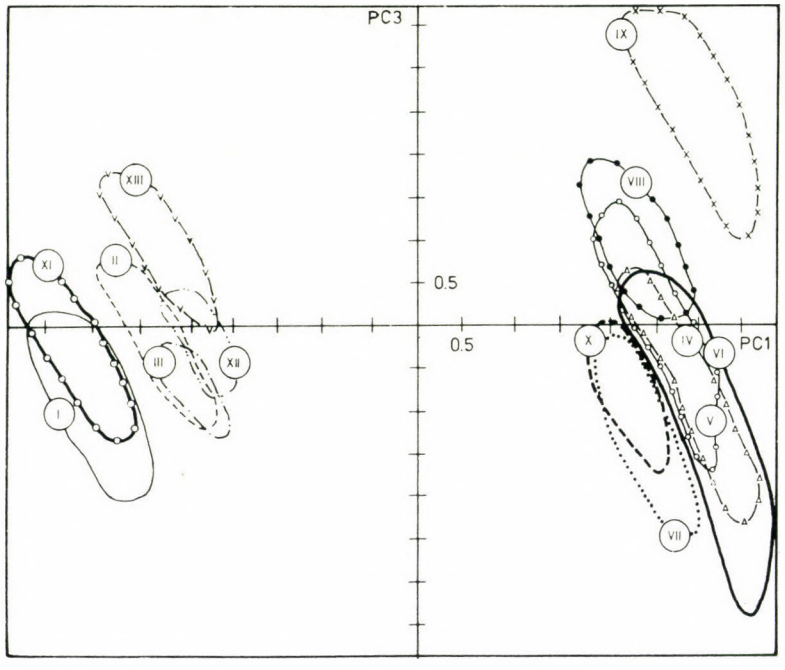

Fig. 5. Principal components ordination of populations on PC1 and PC3. See Table 1 for numbers

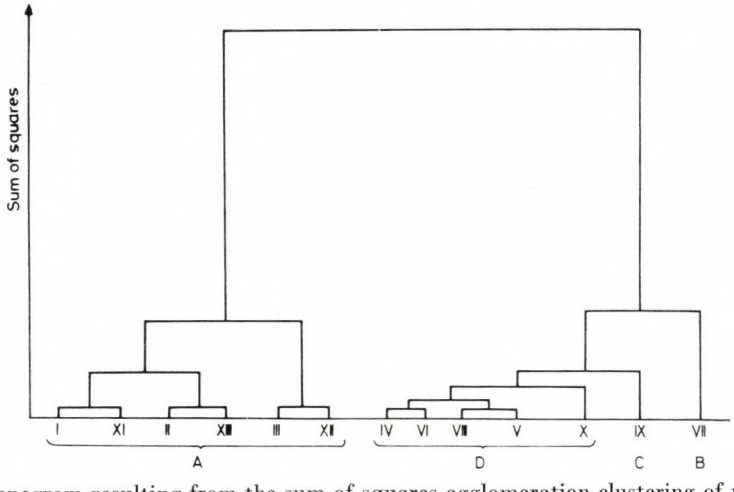

Fig. 6. Phenogram resulting from the sum of squares agglomeration clustering of populations coming from thirteen regions of Hungary. See Table 1 for numbers

Discussion

The numerical analysis of *Scilla bifolia* sensu lato populations collected in Hungary proved the existence of distinct forms. The results of principal component analysis and cluster analysis suggest that at least three, possibly four, taxa can be distinguished within the aggregate. These are designated by A–D in the sequel (see also Fig. 6). The karyotype, most binary and some quantitative characters and both phenological characters appear of fundamental importance in determining group structure.

Group A contains the populations from the upper and middle floodplain of the Danube, from Mecsek, the Villányi Mountains, the foothills of Bakony, and from Békés county. All individuals in this group are diploid ($2n = 18$). Character states typical of these populations are: elaisomes smooth and cylindrical (sausage-shaped), tepals white spotted, dry seeds light ochre, stem buds bluish grey, premature fruits reddish. First day of flowering before 31 March, early leaf marcescence. The mature seeds are approximately 1.5 times longer than in groups B–D. The number of seeds per fruit is 16 on the average. Apparently, this group corresponds to *S. vindobonensis* described by SPETA (1974).

Groups B–D may be clearly distinguished from group A. The main differences are: elaisomes grained, mature seeds dark coloured, tepals always blue. Premature fruits usually green, later turning into brown. The stem buds are also green. Late leaf marcescence and flowering.

The two populations collected in Zemplén constitute group B. Although the chromosome number is 18, just like in group A, the morphological differences are clear-cut, as described above. This group is separated from groups C and D on the basis of a constant leaf number (2), relatively short filaments if compared to the tepals, and of the consistently low seed number (6–7) per fruit. This form seems to be identical with *S. kladnii* Schur, which has originally been described on the basis of the reduced number of seeds.

The plants in group C, collected in western Transdanubia (IX), are tetraploid ($4n = 36$). The morphological characteristics in which this group differs from the others are: stems green and the leaf ratio is low, i.e., the leaves are relatively short and wide. It is doubtful whether this form can be identified as *S. drunensis* Speta (cf. SPETA 1977).

The karyotype of group D, which includes the populations from the Börzsöny and Bükk Mts, Tolna County and the Hortobágy National Park, is also tetraploid. The only exception is the population collected in the Velencei Mts, which is hexaploid. Interestingly, this difference is not manifested in macromorphology. The hexaploid population cannot be distinguished from most tetraploids on the basis of characters included in this study. The number of leaves in this group is commonly three. Numerous (over 20) but small seeds

are found in each fruit. This group is likely to correspond to *S. buekkensis* Speta (1977), formerly listed as *S. subtriphylla* Schur.

In summary, the following conclusions can be drawn from the present study:

1. The striking difference between the diploid and polyploid populations of the *S. bifolia* aggregate suggest their taxonomic disjunction at the species level. Moreover, two diploid species may be found in Hungary, one of them (which is probably *S. kladnii*) being more similar to the tetraploids than to the other diploids.

2. The diploid group A (*S. vindobonensis*) can not be unambiguously subdivided.

3. It seems clear from the results that the polyploid populations in Hungary do not separate from each other at species level. Nevertheless, the taxonomic status of the populations from western Transdanubia remains problematic. Further studies are needed to elucidate its relationship to *S. buekkensis* and *S. drunensis*. On the other hand, the hexaploid population exhibits no demonstrable differences from most tetraploids. Consequently, chromosome number itself is not a reliable basis for creating taxonomic categories within this aggregate.

4. Altitude has no practical influence on the distribution of groups A and D. Both types occur in lowland and mountain habitats.

5. Principal component analysis proved to be a robust technique in indicating group structure. The obvious non-linearity of many characters had no apparent influence on the results, as far as the groups recognized by cluster analysis are concerned.

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SPATIAL DEPENDENCE OF PLANT POPULATIONS

PART 2. A FAMILY OF NEW MODELS*

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This paper attempts to show that equivalence analysis belongs to a family of models, where certain basic concepts and corresponding statistical estimates play a key role in translating propositions of one construction to another. This kind of semantic translation is important, because it guarantees the more or less unified treatment of such different basic phenomena as diversity, resemblance, preference, etc., important in vegetation research.

VIII. Introductory notes

VIII.1 In the first part of this series of papers, an operational extension of *the attribute duality principle* and a related methodology, called *equivalence analysis* have been outlined (JUHÁSZ-NAGY 1976). The main purpose of such analyses is to study "*orderliness*" of different kinds.

VIII.2 As it has already been emphasized, however, orderliness of any kind depends on a number of conditions (e.g. due to sampling, evaluation, etc.) to a considerable extent. Clearly, several further aspects of study are to be clarified, with special reference to *spatial processes* (see VII.). The main aim of this paper is to present a collection of constructions (models), rich enough to cope with at least a part of our difficulties due to "context-dependence", viz. model-dependence (see 0.).

VIII.2.1 The primary purpose of the present paper is to show that even if *the simplest possible conditions* are applied (e.g. *binary* variables are used, *classical* probability fields are assumed, etc.), several types of arguments are possible to model different aspects of study (like *diversity*, *resemblance*, etc.). Note further that, due to strange historical reasons, *the mutual interpretation* of the basic phaenomena in most cases is still very difficult. (For instance, during the development of *numerical syntaxonomy*, some type of *resemblance* has always been "overemphasized", while *diversity* has been practically neglected for a long period.) Therefore, the secondary purpose of the present paper is to show how these simple constructions are related inherently to each other, forming a family (or, sometimes, even a system) of models, where the meaning of one model can safely be translated to the meaning of the other model.

VIII.2.2 This kind of mutual interpretability is important, because at the present state of vegetation research *some* "*semantic gaps*" seem to be even more alarming than beforehand. There exists, for instance, a huge "*terra incognita*" between syntaxonomy and synmorphology (e.g. pattern analysis). If we can say that the most difficult and pertinent problems of vegetation research (such as a deeper understanding of succession and degradation) lie *in the interface of syntaxonomy, synmorphology, and syndynamics*, represented by the inter-

* See Part 1. in Acta Bot. Acad. Sci. Hung. **22:** 61–78 (1976).

section of Fig. 1, then all efforts should be made to clarify that interface as intensely as we can. In order to sharpen this statement even further, suppose that we want to understand in the future *dendrogenesis* [in terms of ERDŐS and RÉNYI (1960): a type of "*graph evolution*"], where *a dendrite* (say, a cluster dendrite) changes in space, or in time, or in a proper spatio-temporal referential system (see Fig. 2). Because any dendrite (a topological tree) is a certain

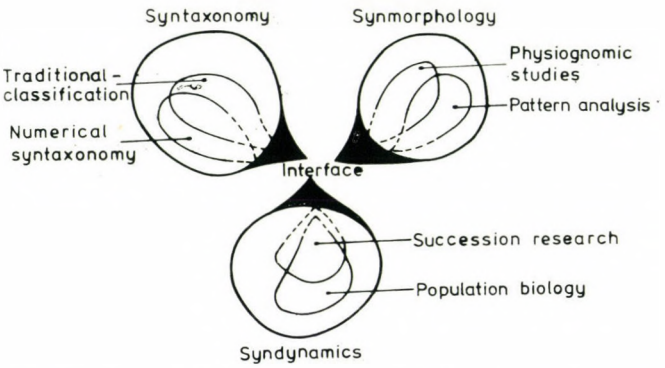

Fig. 1. The importance of three subdisciplines and their interface (see VIII.2.2)

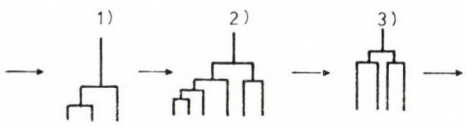

Fig. 2. A possible dendrogenesis (see VIII.2.2)

type of structure, and because a cluster dendrite results in some taxonomic algorithms, the study of a cluster dendrite belongs simultaneously to the realms of both synmorphology and syntaxonomy. Clearly, any prudent interpretation of some dendrogenesis can be made possible, if these realms will be properly interconnected with the third realm of syndynamics (i.e. *the* "*processing aspect*" of the problem). At the present stage of ignorance, it is very difficult to answer the simple question: at what size of plots a certain (say, maximum) degree of interconnectedness might be expected?

VIII.3 This paper deals with problems simpler than dendrogenesis, and has some carefully chosen other limitations as well (see part 1; VIII.2.1; IX.; etc.). Only models interpretable in terms of information theory are used, and by the concept "information" is always meant *contingency information* (*sensu* KULLBACK 1959). The terminology tries to follow some of the best foundations in this field (e.g. KHINCHIN 1959, RÉNYI 1962, ACZÉL and DARÓCZY 1975). The attention of the reader is called to some remarkable works (like PIELOU 1974, 1975, 1977; ORLÓCI 1978a), and to a book under preparation (FEOLI, LAGONEGRO and ORLÓCI 1984) that are concerned with several important problems of such modelling in ecology, or in vegetation research.

This paper is dedicated to the memory of prof. A. RÉNYI, who had first encouraged the author to play with information theory functions.

[A] INITIAL FRAMEWORK OF CONCEPTS

IX. Classes of concepts: basic concepts

IX.1 Let Q be a set of plant populations (labelled usually, but not necessarily as "species"), $Q = \{q_1, q_2, \ldots . q_i, \ldots, q_s\}$, living in a τ topographicum. Let T_j be a set of planar sampling units (plots) with j-specification (say, for shape and size), $T_j = \{t_{j1}, t_{j2}, \ldots, t_{jg}, \ldots, t_{jm}\}$, to be laid-out in the area τ', $\tau' \subset \tau$, $t_{jg} \subset \tau'$. By projecting the bodily points of q_i into τ', and gaining the projection set q_i', $q_i' \subset \tau'$, the binary function (an *elementary floristic function*) can be defined as

$$n_{ijg} = \left\{ \begin{array}{l} 1, \text{ if } q_i' \cap t_{jg} \neq \emptyset, \\ 0, \text{ if } q_i' \cap t_{jg} = \emptyset, \end{array} \right\} \qquad \text{(IX; 1)}$$

where $n_{ijg} = 1$ is called *coincidence*, and $n_{ijg} = 0$ is called *incoincidence*. [Clearly, (IX; 1) can be regarded as *an event*, like that of a BERNOULLI trial, with two elementary outputs. The usual notion of "presence — absence" is avoided, because these concepts should be reserved for special cases, like for "presence in a stand".]

IX.1.1 From a theoretical point of view, Q and τ' are regarded as *universal sets* (sets of *all important points*), while sets q_1', q_2', ..., and sets t_{j1}, t_{j2}, ... are *sets of sampling points* by which some statistical relations can be obtained (say, with respect to the DESCARTES space, $Q \times Q$). In this way of reasoning, $q_i \in Q$ is a *universal relation* (presence), while $q_i \in \Phi_{ij}$ (coincidence) is a *sampling relation*, where φ_{ij}, $\varphi_{ij} \subset Q$, is *the flora* (or, florula, if you like it better) of plot t_{jg}.

IX.1.2 Since elements of T_j correspond to the elements of the class (set of subsets) Φ_j, $\Phi_j = \{\varphi_{j1}, \varphi_{j2}, \ldots, \varphi_{jm}\}$, the results of survey sampling can be arranged in *a binary contingency table*, to be called interchangeably either *an elementary table*, [ET], or a K_j (as in part 1., or in X. and the sequel, if a series of such tables is needed). (IX; 2) gives a very simple illustration of an [ET], where $s = 4$, $m = 8$, $Q = \{u, v, w, z\}$,

u	0	0	1	1	1	0	0	1	4
v	1	0	1	1	1	1	0	1	6
w	0	1	0	0	0	0	1	1	3
z	0	0	0	0	0	1	1	0	2
	1	1	2	2	2	2	2	3	15

(IX; 2)

IX.2 It is fairly important to regard even such a primitive thing as (IX; 2) from the point of view of *classes of concepts*.

IX.2.1 For the sake of simplicity, suppose that we distinguish now only three classes of concepts. The class of *fundamental concepts* (like set, relation,

vector, function, graph, etc.) consists of such mathematical terms that are all-important, everywhere in science. The class of *methodological concepts* (like sampling unit, survey sampling, a statistical test, curve fitting, etc.) consists of such terms that make workable (operational) fundamental concepts in a given context. The class of *basic concepts* (like flora, vegetation, floral diversity, interlocally random composition, etc.) consists of terms of a discipline of its own (in our case: vegetation research). We regard a basic concept *operational*, if it is resulted in a proper interconnection of some fundamental *and* methodological concepts. (Of course, it is perfectly true that such "descriptive terms" as formation or habitat, might be as powerful in their own methodological place and role as operational concepts.)

IX.2.2 A basic concept of the operational type has a definite value, if it is somehow *a member of an operational framework of concepts.* In order to illustrate such a framework, let us set up the following series or *ordered concepts:*

⟨1⟩ *local vectors* (row vectors) of an [ET],

$\xrightarrow{①}$

⟨2⟩ *interlocal relations* between row vectors of an [ET],

$\xrightarrow{②}$

⟨3⟩ *interlocal dependence* between two populations of set Q,

$\xrightarrow{③}$

⟨4⟩ *interlocal association* between two populations of Q (or, pairwise comparison of all elements of Q),

$\xrightarrow{④}$

⟨5⟩ *interlocally significant association* based on conditions of ⟨4⟩,

$\xrightarrow{⑤}$

⟨6⟩ *plexus graph*, a random graph whose points (elements of Q) are interconnected only, if conditions for significant association are satisfied at given probability level(-s),

$\xrightarrow{⑥}$

⟨7⟩ *plexus group*, a subset of Q, generated by *a clicque*, a stochastically separate subgraph of the plexus graph.

IX.2.2.1 It can be seen at once that these concepts are really ordered, because any concept is meaningful only with respect to the former ones. It is true even for ⟨1⟩, for which the concepts of IX.1 give meaning [i.e. *arrangement* of values of (IX; 1) in a proper order]. Note, however, that this chain of mutual interpretability is realized because of ①, . . . , ⑥, a number of operations, or, algorithms. ① means only to set up *some* relations on $Q \times Q$, or, even, on $\times_{i=1}^{n} Q_i$. ② implies the essential novelty of *independence hypothesis*, by which interlocal dependence is defined by such relations as ⟨, ⟩, $\leq$, etc. (in general, by "$\neq$"). ③ gives *a function* (e.g. chi^2, contingency information, etc.) whose

estimated values are supposed to characterize the *deviations* from hypothetically independent situations. (4) evaluates these deviational estimates in given conditions (e.g. at certain *probability levels* of confidence). (5) sets up a number of rules (in particular, if the "plexus" is *a coloured graph*) in order to make the construction possible. Finally, (6) gives some "*cutting algorithm*" for a stochastic partitioning of the graph into more or less separable subgraphs.

IX.2.2.2 Order and correspondence in IX.2 shows clearly that such a series of concepts and operations is almost always needed. It is obvious again that the hard-boiled *dominance of traditional names*, such as the devaluated misuse of "*interspecific correlation*" for any kind of interlocal relations (even if, *not r*, correlation coefficient, was estimated) might be extremely misleading. Note, further, that the adjective "interspecific", in a sense, would have been attached to the other type of relations (i.e. *interfloral* relations); the present connotation is due to a rather unfortunate convention. It is slightly ridiculous that *attribute duality* of [ET] is usually stated by means of such dubious jargon-terms (like "number of species", "RAUNKIAER frequecy", *Q*-technique, *R*-technique etc.) that *have no true suggestion whatever* — in particular, for outsiders, or beginners — *on the true nature of dual relations.* (When the author has recently asked a dozen of his friends, working as applied mathematicians in the field of multivariate analysis, nobody was aware of the mysterious meaning of "*Q*", or "*R*"; one mathematician called them "*obscured free-masonic symbols* originated from the proto-chaos of science".)

IX.3 This is the main reason why the author has decided to substitute some traditional terms by such basic concepts which are, at least potentially, able to cope with the difficulties of interpreting dual relations.

IX.3.1 Without repeating the details of notation in II., (IX; 3) gives the highlights, the simplest list of terms for an [ET], or for a K_j of $s \times m$ size:

			plots		Σ 1	Σ 0
		populations	local vectors	floral vectors	(1) local valences	(2) local invalences
			n_{ijg}			
Σ	1		(3) floral valences		N_j	n_j
	0		(4) floral invalences		n_j	sm

(IX; 3)

IX.3.2 First, note the difference among the three adjectives: (a) "*local*", (b) "*floral*", (c) "*floristic*". (a) and (b) is related always to some *row* and *column properties* of a K_j, respectively, while (c) involves *a joint relational meaning*

between some row *and* column attributes, simultaneously. This is why K_j itself (as a whole binary data structure) can be regarded as a binary representation of some *floristic composition*, and why frequency distributions (1)–(4) in (IX; 3) *altogether* can safely be called *floristic marginals*, or, in brief, *f-marginals*. (Note, further, that, *mutatis mutandis*, a similarly simple semantics may be applied to such adjectives as "local", "*faunal*", "*faunistic*" as well.)

IX.3.3 Using the numbers in (IX; 3), *f-marginals* are symbolized as (1) $V_j^{(q)}$, (2) $v_j^{(q)}$, (3) $V_j^{(t)}$, (4) $v_j^{(t)}$. The symbols (5) N_j and (6) n_j refers to *total valence* and *total invalence* of a K_j, respectively. The entropy *estimators* for these quantities are, in order: (1) A_j, (2) a_j, (3) B_j, (4) b_j, (5) C_j, (6) c_j, where, for instance, $c_j = n_j \log n_j$. (Without further comment, "log" always means "$\log_2$", and numerical values will be given in Bits, i.e. properly *weighted bits*.) In the sequel, we need the following simple generalizations:

$$\left.\begin{aligned} A_j + a_j &= \alpha_j, \\ B_j + b_j &= \beta_j, \\ C_j + c_j &= \gamma_j. \end{aligned}\right\} \qquad \text{(IX; 4)}$$

IX.4 As beforehand, relations between *local* and *floral* vectors are called *interlocal* and *interfloral* relations, respectively.

IX.4.1 In order to illustrate some main points, let us consider two exceedingly simple examples, where $s = 3$, $m = 2^s = 8$, $Q = \{u, v, w\}$,

u	0	1	0	0	1	1	0	1	4
v	0	0	1	0	1	0	1	1	4
w	0	0	0	1	0	1	1	1	4
	0	1	1	1	2	2	2	3	12

(IX; 5)

u	1	1	1	1	0	0	0	0	4
v	0	0	0	0	1	1	1	1	4
w	0	0	0	0	1	1	1	1	4
	1	1	1	1	2	2	2	2	12

(IX; 6)

IX.4.1.1 It is easy to see that all the three pairs of populations in (IX; 5) are *interlocally independent*, therefore, (IX; 5), or, any similar construction, like (V; 8), might be called *interlocally random composition*, [IRC]. On the other hand, in (IX; 6) no pair of populations is independent, in an interlocal sense, and this kind of construction might be called an *interlocally dependent composition*, [IDC].

IX.4.1.2 It goes without saying that, while an [IRC] is *unique* (for a given s), [IDC] may be of very different kinds. We guess at first sight that (IX; 6) has, in many respects, a greater degree of orderliness than (IX; 1).

IX.4.2 This sort of comparison is possible at a first instant by estimating *floral diversity* (JUHÁSZ-NAGY 1976), or, as JUHÁSZ-NAGY and PODANI (1983) call it, by *florula diversity*, i.e. by comparing *possible* and *realized floral vectors*.

IX.4.2.1 Let π_q be the *power set* of floral universe Q, i.e. the set of all subsets of Q, $\Pi_q = \{\pi_{j1}, \pi_{j2}, \ldots, \pi_{jk}, \ldots, \pi_{j\omega}\}$, where π_{jk} is a *potential flora*, and $\omega = 2^s$. Let F_j be the frequency distribution for Π_q generated by T_j, $F_j = \{f_{j1}, \ldots, f_{jk}, \ldots, f_{j\omega}\}$. The elements of Φ_j (see IX.1.2) are those element Π_q that are represented in the survey-sampling by non-zero frequency values (*manifested floras*). By supposing that the sampling conditions are satisfactory ($m > s$, $m \to \infty$), and the probability estimate $\hat{p}_{jk}$, $\hat{p}_{jk} = f_{jk}/m$, is more or less unbiased, we can set the up *an empirical finite scheme*,

$$\Pi_{qj} = \begin{bmatrix} \pi_{j1}, \pi_{j2}, \ldots, \pi_{jk}, \ldots, \pi_{j\omega} \\ \hat{p}_{j1}, \hat{p}_{j2}, \ldots, \hat{p}_{jk}, \ldots, \hat{p}_{j\omega} \end{bmatrix} \qquad \text{(IX; 8)}$$

with estimated probability distribution $\hat{p}_j$, related to Π_q, *a complete system of events*. If by letting U_j to be a suitable *estimator* such as $U_j = \sum_k f_{jk} \log f_{jk}$, $\sum_k f_{jk} = m$, then *floral diversity*, $m\hat{H}_j^{(\varphi)}$,

$$m\hat{H}_j^{(\varphi)} = m \log m - U_j, \qquad \text{(IX; 9)}$$

a weighted entropy-estimate of the SHANNON-type can be defined.

IX.4.2.2 It is to be noted that $m\hat{H}_j^{(\varphi)}$ is not only one estimate of the the many similar estimates; it has a number of fairly important properties. The most remarkable feature of $mH_j^{(\varphi)}$ is that floral entropy, as *an "overall uncertainty bound"*, or, more precisely, as *a joint entropy* for *all* elements of Q,

$$m\hat{H}_j^{(\varphi)} = ([q_1, q_2, \ldots, q_i, \ldots, q_s]), \qquad \text{(IX; 10)}$$

contains *all* possible "*regions*", where any kind of "interaction" among populations may take place (see Fig. 3). In other words, $m\hat{H}_j^{(\varphi)}$ is served as an *upper bound* for association estimates, or even, for associatum (see IX.5).

IX.4.2.3 Disregarding at the moment suitable conditions for a satisfactory survey sampling, consider the estimated values of $m\hat{H}_j^{(\varphi)}$ for (IX.1), (IX; 5), and (IX; 6), which are: 19.25, 24, and 8 Bits. It is easy to relate these values to the ratio of "*posse — esse*"; e.g., for any kind of [IRC], like (IX; 5), $m\hat{H}_j^{(\varphi)} = \max mH_j^{(\varphi)} = m \log m$, because all kinds of potential floras are realized. (If, in an [IRC], where $f_{jk} > 1$, then $\max \hat{H}_j^{(\varphi)} = sm$ Bits.)

IX.4.3 If we do not distinguish *all* possible floral vectors, only those vectors whose floral marginal values are the same, we can speak of *floral multiplets*, characterized by a multiplet varable, R, $R = \{0, 1, \ldots, r, \ldots, s\}$ (see II.3). The frequency distribution of R values of a K_j is $F_j' = \{g_{j0}, g_{j1}, \ldots, g_{jr}, \ldots, g_{js}\}$, $\sum_r g_{jr} = m$, and the frequency distribution of the weighted R values

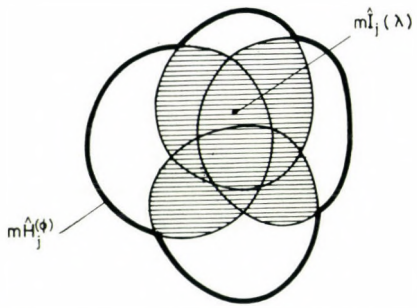

Fig. 3. Associatum $(m\hat{I}_j(\lambda))$ is a measurable subset of the intersection in a VENN-diagram, whose bound is $m\hat{H}_j(\Phi)$, floral diversity

is F''_j, $F''_j = \{g'_{j1}, g'_{j2}, \ldots, g'_{jr}, \ldots, g'_{js}\}$, $g'_{jr} = rg_{jr} = n._{jr}$, $\sum rg_{jr} = N_j$. By introducing suitable estimators, G_j for F'_j, and E_j for F''_j, $G_j = \sum_r g_{jr} \log g_{jr}$, $E_j = \sum_r n._{jr} \log n._{jr}$, we can define

$$m\hat{H}_j(R) = m \log m - G_j, \qquad \text{(IX; 11)}$$

$$N_j\hat{H}_j(V_R) = C_j - E_j. \qquad \text{(IX; 12)}$$

Both estimates, in particular, $N_j\hat{H}_j(V_R)$, *entropy of floral multiplets for valence values*, will be used in the sequel (see e.g. XI.1).

IX.5 Finally, the reader is reminded of *associatum* (cf. JUHÁSZ-NAGY et al., 1973, JUHÁSZ-NAGY 1976, JUHÁSZ-NAGY and PODANI 1983),

$$m\hat{I}_j(\lambda) = sm \log m - \alpha_j - m\hat{H}_j^{(\varphi)}, \qquad \text{(IX; 13)}$$

a multiple contingency information, i.e. contingency information estimate of a $2 \times 2 \times \ldots^{s} \times 2$ table. Since, with respect to (IX; 14),

$$m\hat{I}_j(\lambda) = ([q_1, q_2, \ldots, q_i, \ldots, q_s]), \qquad \text{(IX; 14)}$$

the relation between $m\hat{H}_j^{(\varphi)}$ and $m\hat{I}_j(\lambda)$ can easily be shown by a VENN-diagram (see fig. 3).

X. Some basic relations: spatial processes

X.1 Suppose that elements of T_j are circular plots, to be randomized over τ'. Suppose, further, that we have a class of plots, Θ_h, $\Theta_h = \{T_0, T_1, \ldots, T_j, \ldots, T_u\}$, where elements of T_0 are approximately "points", and the size of plots increases from T_0 to T_u, in a strictly monotonous way. More precisely,

if the size of plots are labelled as $t_0, t_1, \ldots, t_j, \ldots$, then the increasing series $t_0 < t_1 < \ldots < t_j < \ldots$ is the first feature of the survey sampling below. (It should be noted that, while the symbol t_{jg} indicates an element, $t_{jg} \in T_j$, as *an entity*, the symbol t_j refers to the geometric size of this element.)

X.1.1 Of course, this increasing series may be of very different kinds. If we define the difference between t_j and t_{j-1} as an interval, $| t_j, t_{j-1} |$, or, give rule to generate such differences, we can speak of several types of *articulation* of sampling. If the articulation is "rough", then the strictly monotonous series, $N_0 < N_1 < \ldots < N_j < \ldots$, and, $n_0 > n_1 > \ldots > n_j > \ldots$ are likely to be expected. If the articulation is "fine" enough, then the relations $N_j \leq N_{j+1}$, $n_j \geq n_{j+1}$, might occur, i.e. the series are *not* strictly monotonous.

X.1.2 The choice of articulation should depend on the particular object (vegetation-type), and on the purpose of the investigator. (Unfortunately enough, *a priori*, before making a survey sampling, we do not know in most cases the "resolutional properties" of our object, which shows clearly the need of *an iteration*, viz. *successive approximation*.) Experience suggests that a "good articulation" must not be "monotonously regular", because of the existence of some "critical regions".

X.2 In order to illustrate some primary points of this paper, it is worthwhile to consider a concrete example, and derive certain primary conclusions from it. Similar examples are given by JUHÁSZ-NAGY and PODANI (1983).

X.2.1 The particular type of vegetation is *a meadow*, in NE-Hungary (near the village Beregdaróc) which has been described by the author, on the top of his SIGMA-tist period, as *Anthoxantho-Festucetum pseudovinae, festucetosum sulcatae* (JUHÁSZ-NAGY, 1958), where $s = 83$, $m_1 = 256$, $m_2 = 512$, due to two survey samplings. The long and tedious sampling procedures have been established twice (May, 1965 and 1966); the second survey has been aimed at correcting some results of the first one. (This is why $m_2 > m_1$.) Some details about survey sampling are considered later on.

X.2.2 Let $R_j^{(1)}(\lambda)$ be *a redundancy estimate*, called *simple relative associatum*,

$$R_j^{(1)}(\lambda) = 1 - m\hat{I}_j(\lambda)/m\hat{H}_j^{(\varphi)}, \qquad (X; 1)$$

which has a fairly good intuitive meaning with respect to fig. 3. Roughly speaking, (X; 1) relates associatum to an "overall uncertainty bound". (The upper index (1) in (X; 1) distincts *this* redundancy estimate from better ones, that can be considered later, on when the boundary relations of $m\hat{I}_j(\lambda)$ will be clarified.)

X.2.3 The curve of Fig. 4 shows *change of the redundancy estimate in space* with respect to our meadow of X.2.1. We can see at once two peaks of the curve, indicating two local maximum points of $R_j^{(1)}(\lambda)$. The rough-and-ready interpretation of such curves is possible, if we suppose that while the first

peak is due to the "dominance of *negative* associations", the position of the second peak may due to the "dominance of *positive* associations". Indeed, the position of the first peak corresponds surprisingly well to the first maximum of $m\hat{I}_j(\lambda)$, and to the local maximum of pooled negative interlocal associations. The second peak of fig. 4, however, has no such well-defined correspondences, except that it is located fairly closely to A_{comp}, *conpensatory area*, where

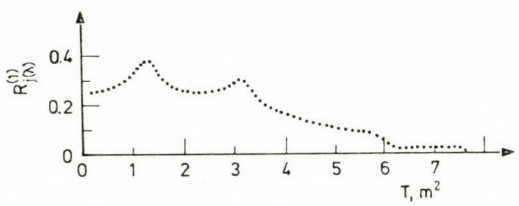

Fig. 4. An $R_j^{(1)}(\lambda)$ *versus* T curve (see X.2.3)

$N_j \approx n_j$. Besides some arguments to be explained later on, it is not too difficult to recognize that such a tranformation in most cases is necessary, because $m\hat{I}_j(\lambda)$ converges more quickly to zero than $m\widehat{H}_j^{(\varphi)}$, and, therefore, $R_j^{(1)}(\lambda)$ reaches zero before *a minimum area*, $A_{\min}$, where $N_j = ms$, $n_j = 0$. It is to be observed that *maximum area*, $A_{\max}$, local maximum of $mH_j^{(\varphi)}$, is located between the two peaks of Fig. 4.

X.3 In the case of Fig. 4, or in a number of similar cases, we deal with *a spatial process* of the simplest type, i.e. with a discrete approximation of an almost continuous graphicon. (The second survey was made to control wheather the curve is "smooth" enough, there is no third peak, etc.) In order to discuss such spatial processes of the floristic type, the following *terms* are proposed for further use.

X.3.1 Let us call such functions as $m\widehat{H}_j^{(\varphi)}$, $m\hat{I}_j(\lambda)$, $R_1^{(1)}(\lambda)$ etc. *characteristic functions.* (Note that here the adjective "characteristic" is used, of course, in a special *methodological sense* of the word, i.e. the present meaning should be kept clearly distinct from the meaning of "characteristic functions" of the mathematical analysis, *alias*, "calculus".) The *extremal values* of characteristic functions (maxima, minima) indicate certain *characteristic points* of T, corresponding in our case to a number of *characteristic areas* (e.g. $A_{\max}$, A_{comp}, $A_{\min}$, etc.). A proper inequality, such as

$$\ldots A_{\text{ass}}^{(1)} < A_{\max} < A_{\text{comp}} < \ldots \qquad \text{(X; 2)}$$

shows some *characteristic ordering* of characteristic points or areas. A characteristic ordering can be made more efficient by defining a number of *characteristic intervals*, such as $| A_{\max}, A_{\text{comp}} |$, etc.

X.3.2 It is quite obvious that the characteristic interval $| t_0, A_{\min} | = T$, called the *floristic scale* (in brief, *the scale*) has the important property that T contains (by relation $\in$, or by $\subset$) *all* relevant characteristic points or intervals. $A_{\min}$, in many cases exists, but it may be *trivial*, if $A_{\min} \approx \mu(\tau')$, where the symbol $\mu(\tau')$ indicates the size of the study area. A non-trivial $A_{\min}$ exists, if $A_{\min} \ll \mu(\tau')$. (In our case, for instance, where the study area, viz. *stand* area of the meadow is about 60 000 m^2 in size, and since this area is surrounded by forests and swamps, we can safely say that a non-trivial $A_{\min}$ exists.) There are cases, where there is no well-defined $A_{\min}$, but a scaling point t_u can be found from which all information estimates (defined floristically) converge stochastically to zero.

X.4 During a survey sampling, that is operating with such *scaling points* as t_j, $t_j \in T$, our intention is to make *a characteristic scaling*, or, at a more advanced level, *a characteristic screening*. Both *searching procedures* attempt to locate certain characteristic values (points, or intervals) in the scale, but while in a scaling procedure we want to study *some* synmorphological features of a community, during a screening procedure we have some specific *desideratum* in mind, e.g. we would like to locate *the optimal interval* of the scale for a certain classificatory algorithm. (The personal guess of the author is that some interval around the point given by the first local maximum of $m\hat{I}_j(\lambda)$, $A^{(1)}_{\text{ass}}$, might be optimal for a number of classificatory procedures.)

X.4.1 The primary concern of any characteristic scaling is to consider some bounds of the estimators, e.g.

$$\left.\begin{aligned} N_j \log \overline{m}_j \leq A_j \leq N_j \log m \\ N_j \log \overline{s}_j \leq B_j \leq N_j \log s \end{aligned}\right\} \qquad \left.\begin{aligned} n_j \log (m - \overline{m}_j) \leq a_j \leq n_j \log m \\ n_j \log (s - \overline{s}_j) \leq b_j \leq n_j \log s \end{aligned}\right\} \qquad \text{(X; 3)}$$

where $\overline{m}_j = N_j/s$, $\overline{s}_j = N_j/m$, or,

$$\left.\begin{aligned} (\gamma_j - ms \log s) \leq \alpha_j \leq sm \log m \\ (\gamma_j - sm \log m) \leq \beta_j \leq ms \log s \end{aligned}\right\} \qquad \text{(X; 4)}$$

These simple bounds will be frequently used in the sequel (see e.g. XII.2).

X.4.2 As for the primary meaning of such bounds, we can reconsider some statements made in IV. If a K_j is in an l-state, then A_j has its value at the lower bound; if a K_j is in an L-state, then A_j has its maximum value. (*Mutatis mutandis*, similar relations are true for all the estimators.) From the point of view of scaling, some states, relatively close to an l-state, can be expected somewhere in certain "mid-regions" (critical intervals) of the scale (except, of course, the irrelevant $A_{\min}$-state). Some object (our meadow, for

instance) has the property, however, of approaching some *l*-state more than once. The presence or absence of this property depends on the "structural complexity" of the community, or, speaking in simpler terms, on the *scoring* (floristic) *diversity states* of the object that can be traced by means of some functions defined on a series of K_0, K_1, ..., K_j, ... (see XII.3.2; XIII., etc.).

X.4.3 These relations indicate again the need for a better understanding of such concepts as *orderliness*, *equivalence information*, etc. This need is stressed further by the fact that, contrary to the naive belief of many investigators, some *maximum* degree of entropy *and* information estimates might be very closely located in the scale. Without repeating notation and arguments used in part 1, the reader is reminded of ⟨1⟩-table and ⟨0⟩-table, for wich $N_j\hat{I}_j(E)$ and $n_j\hat{I}_j(e)$ can be related.

XI. Equivalence information – revisited

XI.1 In order to study again $N_j\hat{I}_j(E)$ more closely, let

$$\left.\begin{array}{ll} (1) & N_j\hat{H}_j(V_q) = C_j - A_j, \\ (2) & N\hat{H}_j(V_R) = C - E_j, \\ (3) & N_j\hat{H}_j([V_q, V_R]) = C_j - D_j, \end{array}\right\} \qquad \text{(XI; 1)}$$

where (1) is *entropy of local valences* (cf. XII.1), (2) is *entropy of floral multiplets for valence values* (cf. IX.4.3), and (3) is *equivalence entropy* (a special kind of *joint entropy*), by which

$$N_j\hat{I}_j(E) = N_j\hat{H}_j(V_q) + N_j\hat{H}_j(V_R) - N_j\hat{H}_j([V_q, V_R]) = \\ = C_j - A_j - E_j + D_j \qquad \text{(XI; 2)}$$

as in (II; 5). Using this new notation in hand, it is straightforward to introduce the corresponding pair of *conditional entropy functions*:

$$\left.\begin{array}{l} N_j\hat{H}_j(V_q \mid V_R) = E_j - D_j, \\ N_j\hat{H}_j(V_R \mid V_q) = A_j - D_j. \end{array}\right\} \qquad \text{(XI; 3)}$$

This pair of function almost always play a fairly important role in understanding orderliness of different types, because

$$N_j\hat{H}_j(V_q) - N_j\hat{H}_j(V_q \mid V_R) = N_j\hat{H}_j(V_R) - N_j\hat{H}_j(V_R \mid V_q) = N_j\hat{I}_j(E). \quad \text{(XI; 4)}$$

XI.2 In the case of an [IRC] (cf. IX.4.1.1), where, according to the proof given in V.2.4, the equality $C_j - A_j = E_j - D_j$ is always true, and,

therefore, the equations of (XI; 5)

$$\begin{aligned} N_j\hat{H}_j(V_q) &= N_j\hat{H}_j(V_q \mid V_R) \\ N_j\hat{H}_j(V_R) &= N_j\hat{H}_j(V_R \mid V_q) \\ N_j\hat{H}_j(V_q) + N_j\hat{H}_j(V_R) &= N_j\hat{H}_j([V_q, V_R]) \end{aligned} \qquad \text{(XI; 5)}$$

make clear that $N_j\hat{I}_j(E) = 0$ for any [IRC], i.e. the stochastic independence of events $[q]$ and $[R]$. Note that conditions of (XI; 5) correspond naturally to the maximum value of $m\hat{H}_j^{(\varphi)}$ and to the minimum (zero) value of $m\hat{I}_j(\lambda)$.

XI.2.1 More precisely, by applying the proper PASCAL-triangle rule (cf. V.4), and by letting $s_r = \binom{s-1}{r}$, $\Delta_s = \sum_r \sigma_r \log \sigma_r$, $s^* = \log s$, a fairly concise description of estimators is possible,

$$\begin{aligned} C_j &= s(s + s^* - 1)\, 2^{s-1}, \\ A_j &= s(s - 1)\, 2^{s-1}, \\ D_j &= s\Delta_s, \\ E_j &= s(s^* 2^{s-1} + \Delta_s), \end{aligned} \qquad \text{(XI; 6)}$$

and, using (XI; 6), we get (XI; 7),

$$\left.\begin{aligned} N_j\hat{H}_j(V_q) = N_j\hat{H}_j(V_q \mid V_R) &= ss^*\ 2^{s-1}, \\ N_j\hat{H}_j(V_R) = N_j\hat{H}_j(V_R \mid V_q) &= s[(s-1)2^{s-1} - \Delta_s], \\ N_j\hat{H}_j(V_q \mid V_R) + N_j\hat{H}_j(V_R \mid V_q) = N_j\hat{H}_j([V_q, V_R]) &= \\ = s[(s + s^* - 1)2^{s-1} - \Delta_s], & \end{aligned}\right\} \qquad \text{(XI; 7)}$$

i.e. the detailed verification of (XI; 5). Since $N_j\hat{I}_j(E) = 0$, thus $\hat{Y}_j = N_j\hat{I}_j(K)$; $N_j\hat{I}_j(K) = ss^*2^{s-1} - B_j$.

XII.2.2 For an [IRC], where $s = 3$, as in (IX; 5), $C_j = 43.0188$, $A_j = 24$, $E_j = 25.118$, $D_j = 6$, and so $N_j\hat{H}_j(V_q) = N_j\hat{H}_j(V_q \mid V_R) = 19.0188$, $N_j\hat{H}_j(V_R) = N_j\hat{H}_j\ (V_r \mid V_q) = 18$, $N_j\hat{H}_j\ (V_q \mid V_r) + N_j\hat{H}_j(V_r \mid V_q) = N_jH_j\ ([V_q, V_R]) = 37.0188$, $\hat{Y}_j = N_j\hat{I}_j(K) = 8.2641$. Note that as s increases, the difference of $N_j\hat{H}_j(V_q)$ and $N_j\hat{H}_j(V_R)$ increases as well. Note, further, that by dropping the notation of (XI; 6), we can express $\hat{Y}_j = N_j\hat{I}_j(K)$ as $N_j \log s - B_j$ (see XIV.3.2).

XI.3 On the other hand, if a K_j represents an [IDC] of some sort, where $m\hat{I}_j(\lambda) > 0$, the particular K_j might be of very different kinds, according to the conditions for orderliness involved. For further use, let us distinguish here only two kinds of compositions.

XI.3.1 In an at least locally *well-ordered case*, where $A_j = D_j = N_j \log s$, $E_j = B_j + D_j$, that is, $N_j\widehat{H}_j(V_q \mid V_R) = C_j - D_j = N_j \log m_j$, $N_j\widehat{H}_j(V_R \mid V_q) = 0$, $N_j\widehat{H}_j(V_q \mid V_R) = N_j\widehat{H}_j([V_q, V_R])$, and, therefore, $\widehat{Y}_j = 0$, $N_j\hat{I}_j(E) = N_j\hat{I}_j(K) = C_j - E_j$. In words, this means that the measurable subset of joint entropy that represents intersection will be identical with the whole set of $N_j\widehat{H}_j(V_R)$; this is why $N_j\widehat{H}_j(V_R \mid V_q) = 0$.

XI.3.2 In an at least locally *ill-ordered case*, where $C_j = E_j$, $A_j = D_j = N_j \log s$, $B_j = N_j \log m$, that is, $N_j\widehat{H}_j(V_q \mid V_R) = E_j - D_j$, $N_j\widehat{H}_j(V_R) = N_j\widehat{H}_j(V_R \mid V_q) = 0$, and, therefore, $\widehat{Y}_j = N_j\hat{I}_j(K) = N_j \log \overline{N}_j$ (see e. g. XIV.2.2), consequently, $N_j\hat{I}_j(E) = 0$. In words, this means that because one of the entropy estimates in (XI; 2) completely disappears, the intersection should be "empty"; this is why the value of equivalence information is zero.

XI.4 Although our understanding of orderliness became perhaps a bit more advanced, a branch of new problems arise, if, *ad analogiam* of (XI; 2), we introduce such new estimates as

$$\left.\begin{aligned} n_j\widehat{H}_j(v_q \mid v_R) &= e_j - d_j, \\ n_j\widehat{H}_j(v_R \mid v_q) &= a_j - d_j, \\ n_j\widehat{H}_j([v_q, v_R]) &= c_j - d_j, \end{aligned}\right\} \qquad \text{(XI; 8)}$$

and start asking questions about such additive relations as

$$\left.\begin{aligned} &N_j\hat{I}_j(E) + n_j\hat{I}_j(e) = ms\hat{I}_j(\varepsilon) = \gamma_j - \alpha_j - \varepsilon_j + \delta_j, \\ &N_j\hat{I}_j(K) + n_j\hat{I}_j(k) = ms\hat{I}_j(X), \\ &\widehat{Y}_j + \widehat{y}_j = \widehat{\eta}_j = \varepsilon_j - \delta_j - \beta_j, \end{aligned}\right\} \qquad \text{(XI; 9)}$$

where $\varepsilon_j = E_j + e_j$, $\delta_j = D_j + d_j$. We might guess that a proper interpretation of (XI; 8) is possible within the framework of *syncretic models*, where coincidences *and* incoincidences of *all* elements of a K_j are considered altogether,

[B] SOME SYNCRETIC MODELS

XII. Marginal diversity functions

XII.1 Let us define the following *weighted entropy functions* on the f-marginals of a K_j, referring to marginal uncertainty estimates at t_j,

$$\left.\begin{aligned} &(1)\quad N_j\widehat{H}_j(V_q) = C_j - A_j, \\ &(2)\quad N_j\widehat{H}_j(V_t) = C_j - B_j, \\ &(3)\quad n_j\widehat{H}_j(v_q) = c_j - a_j, \\ &(4)\quad n_j\widehat{H}_j(v_t) = c_j - b_j. \end{aligned}\right\} \qquad \text{(XII; 1)}$$

XII.1.1 If, for the sake of brevity, we label here entropy function by [EF], then (1) is [EF] of *local valences* (cf. XI.1), (2) is [EF] of *floral valences*, (3) is [EF] of *local invalences*, and, (4) is [EF] of *floral invalences*. Functions (1) and (2) are monotonously *increasing*, functions (3) and (4) are monotonously *decreasing* in the spatial process described in X.

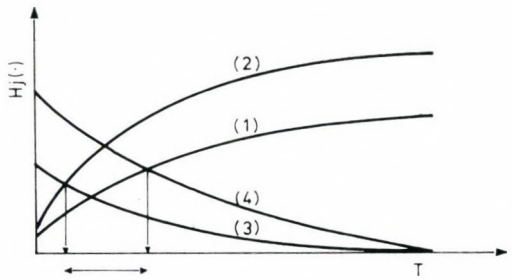

Fig. 5. A quartet of "species area curves", according to (XII; 1) (see XII.1.2)

XII.1.2 More precisely, if a non-trivial $A_{\min}$ exists, then (1) and (2) reaches (or, at least, stochastically converges to) its maximum of $ms \log s$ and $sm \log m$, respectively, while (3) and (4) tends to zero *within* the size of a τ'. Because of this property (monotony), functions of (XII; 1) cannot be used as "diversity indeces" (see GRASSLE et al. 1979). These functions, however, might be the optimal substituents of the classical "*species-area curves*" used so far in many respects. It is remarkable that in the majority of cases the interval of scale, whose extremal points are located, where the approximate equalities of $N_j H_j(V_t) \approx n_j \widehat{H}_j(v_q)$ and $n_j \widehat{H}_j(v_t) \approx N_j \widehat{H}_j(v_q)$ are satisfied, includes practically *all the important characteristic points* (except, of course, $A_{\min}$) that may be interesting in vegetation research (see Fig. 5). The search for such *a maximum interval* (as *a characteristic interval*) is perhaps the simplest way of indicating the *size-classes* within which a *reasonable survey sampling* can be taken. Besides, the curves of Fig. 5 can frequently be linearized as special "*synallometric*" (log-linear) *curves*. (This topic should be treated elsewhere.)

XII.2 The best property of functions in (XII; 1) is that they are all bounded by the the following simple inequalities [cf. (X; 3) etc.],

$$\begin{aligned}
&(1)\quad N_j \log \bar{s}_j && \leq N_j \widehat{H}_j(V_q) \leq N_j \log s \\
&(2)\quad N_j \log \bar{m}_j && \leq N_j \widehat{H}_j(V_t) \leq N_j \log m \\
&(3)\quad n_j \log (s - \bar{s}_j) && \leq n_j \widehat{H}_j(v_q) \leq n_j \log s \\
&(4)\quad n_j \log (m - \bar{m}_j) && \leq n_j \widehat{H}_j(v_t) \leq n_j \log m
\end{aligned} \qquad \text{(XII; 2)}$$

where, again, $\bar{s}_j = N_j/m$ (i.e. local mean density), $\bar{m}_j = N_j/s$ (floral mean density) as in IV.

XII.3 According to inequalities in (XII; 2), both *upper deviates*.

$$\Delta N_j\widehat{H}_j(V_q) = \max N_jH_j(V_q) - N_j\widehat{H}_j(V_q) = N_j \log s + A_j - C_j,$$
$$\Delta N_j\widehat{H}_j(V_t) = N_j \log m + B_j - C_j,$$
$$\Delta n_j\widehat{H}_j(v_q) = n_j \log s + a_j - c_j, \qquad \text{(XII; 3)}$$
$$\Delta n_j\widehat{H}_j(v_t) = n_j \log m + b_j - c_j,$$

and *lower deviates*,

$$\nabla N_j\widehat{H}_j(V_q) = N_j\widehat{H}_j(V_q) - \min N_jH_j(V_q) = N_j \log m - A_j,$$
$$\nabla N_j\widehat{H}_j(V_t) = N_j \log s - B_j,$$
$$\nabla n_j\widehat{H}_j(v_q) = n_j \log m - a_j, \qquad \text{(XII; 4)}$$
$$\nabla n_j\widehat{H}_j(v_t) = n_j \log s - b_j,$$

as empirical *gain of information* estimates at t_j (see KHINCHIN 1959) indicate how diverse *f*-marginals are. Contrary to (XII; 1), functions in (XII; 3) and (XII; 4) represent *useful diversity functions* (called *marginal diversity functions*) based on the simple reasoning as follows.

XII.3.1 If K_j is in *a monovalence state* of either kind, or both kinds, then proper *upper deviate* (or deviates) has (or have) zero value. On the other hand, in the same case, the proper *lower deviates* are represented by their *maximum* values. If K_j is in *an oligovalence state*, then, *vice versa*, *upper* and *lower* deviates take their *minimum* and *maximum* values, respectively.

XII.3.2 This shows clearly that *all* the eight deviates (in short, *the octet*) should be used *altogether*, in order to characterize *the marginal diversity state* of a K_j. In addition, *f*-deviates, i.e. members of octet play an important role in composing information estimates, because each contingency information can be gained as the sum of the proper gain of information estimates (see XIII—XIV.).

XIII. Three partners modelling

XIII.1 It is sometimes very useful to think of a K_j as an output of a situation resulted in *a three-ways selection*. Because any selection is *a repetitive choice* of some kind, our elementary concept should be (IX; 1), *a random choice*, which henceforth will always be called *an intersection*. (Note that the very general meaning of set operation $\cap$ is substituted here by a particular *methodological meaning* of the word.) Let us define three "*abstract partners*",

an average population (q), *an average plot* of j-size (t), and *an average intersection* (i), related to the ordered pair $\langle q, t \rangle$. All partners are endowed with selective property, namely,

— q selects *plots* from the elements of T_j,
— t selects *populations* from set Q,
— i selects *ordered pairs* from ms possibilities.

XIII.1.1 In this *selective situation*, a fairly good intuitive framework might be introduced. For instance, besides *choice* and *selection* (represented by the "inner" scalars and vectors of a K_j), we can rightly think of "*selectional powers*" of partners (shown by the f-marginals of a K_j), or of *diversity of selectional powers* (characterized by an *octet*). Since selection of some sort is always related to a certain degree of *preference*, we might think of our selective situation as of *a preferential situation* as well. For instance, in an [IRC], where no kind of local, or interlocal preference is present, all properties of an [IRC] (l-state, max $mH_j^{(\varphi)}$, zero-valued $m\hat{I}_j(\lambda)$, etc.) are due to this lack of preference. Note, further that a huge number of old notions (e.g. ubiquity, commonness, rarity, constancy, fidelity etc.) is closely related to such an intuitive framework of concepts. These concepts, however, have a strong "historical load", and this is responsible for a number of misunderstanding (JUHÁSZ-NAGY 1964).

XIII.1.2 For the reasons why is it plausible to allow for either t or i to have *selectional powers*, we may turn to several generalizations of our situation, e.g. where Q can be a set of *animals*, *enzymes*, etc., T_j can be a set of some *foods*, *substrates*, etc., at a given j-condition, say, at a given degree of temperature. Although elements of Q, without doubt, are "more active" than elements of T_j, *plots*, *foods*, *substrates* (simply, by virtue of "quality" or j-state they represent) also selects *plants*, *animals*, *enzymes*; this is why such concepts as *enzyme specificity*, *substrate specificity*, and *reaction specificity*, notwithstanding *coplimentary*, but *are by no means related trivially to each other* (see QUASTLER 1953).

XIII.2 According to KOLMOGOROV, assume *a classical probability field* for our selective situation, i.e. $p(q) = 1/s$, $p(t) = 1/m$, $p(i) = 1/ms$, and thus, in terms of information theory, we have

$$\left.\begin{aligned} H(q) &= \log s, \\ H(t) &= \log m, \\ \hat{H}_j(i) &= \log ms - \gamma_j/ms, \end{aligned}\right\} \qquad \text{(XIII; 1)}$$

i.e. quantities of the HARTLEY type (see RÉNYI, 1962; REZA, 1961; LUCE, 1960). Note that even in this utterly simple (say, "hyperprimitive") formalism, the entropy $\hat{H}_j(i)$ can be given as an estimate, only. The primary explanation of this is due to *a particular transition*; namely, the relation $t_{jg} \in T_j$ is trans-

ferred here to the selectional relation of partner i. The same is true for for the corresponding joint entropy functions,

$$\left.\begin{aligned}\hat{H}_j([q, i]) &= \log ms - \alpha_j/ms,\\ \hat{H}_j([t, i]) &= \log ms - \beta_j/ms,\end{aligned}\right\} \qquad \text{(XIII; 2)}$$

$$H([q, t]) = \log ms, \qquad \text{(XIII; 3)}$$

where (XIII.3), *not* containing i, is of constant value, but functions of (XIII; 2) are estimates, related to the actual (j-dependent) values of the estimators involved.

XIII.3 It is fairly easy to see that, having (XIII; 1)—(XIII; 3), a whole system of equations can be obtained, and *some* of these equations have a definite bearing on certain aspects of our selective or preferential situation.

XIII.3.1 According to the simplest kind of a Boolean reasoning, the particular event space is partitioned by (XIII; 1) into $2^3 = 8$ molecular events, and we might consider these events as singletons, doubletons etc., so we have altogether $2^8 = 256$ kinds of functions. (Fortunately enough, the vast majority of these functions is quite irrelevant and immaterial for our present purpose.) This family of functions includes e.g. *conditional entropy functions* (like $H(q \mid t) = H([q, t]) - H(t) = \log s$), *information functions* (e.g. $\hat{I}_j(q, i)$, $\hat{I}_j(t, i)$, etc.), *multiple informations functions* (e.g. $\hat{I}_j(i, [q, t])$, etc.), *partial information functions* (like $\hat{I}_j([q, t] \mid i)$, etc.), and so on.

XIII.3.2 The simplest possible information is

$$I(q, t) = H(q) + H(t) - H([q, t]) = \log s + \log m - \log ms = 0 \quad \text{(XIII; 4)}$$

which has the definite meaning that partners q and t, *without partner* i, have *no information* whatsoever with respect to each other. This indicates clearly that we should concentrate on such functions which include partner i as well. For the sake of convenience, it is much better to use weighted forms (i.e. each function is multiplied by ms).

XIII.4 It is worthwhile investigating *a triplet of functions* (in itself a simple *linear model*) in a little bit more detailed way, and turning afterwards to other relevant functions of the three partner modelling.

XIII.4.1 According to XIII.2,

$$ms\hat{I}_j(q, i) = msH(q) + ms\hat{H}_j(i) - ms\hat{H}_j([q, i]) = ms \log s + ms \log ms - \gamma_j -$$
$$- (ms \log ms - \alpha_j) = ms \log s + \alpha_j - \gamma_j. \qquad \text{(XIII; 5)}$$

It is to be noticed that (XIII; 5) is identical either with contingency information of the little (*local*) contingency table" on the right side of an [ET], or

with the sum of the proper *upper* deviates in (XII; 3):

$$ms\hat{I}_j(q, i) = \Delta N_j \hat{H}_j(V_q) + \Delta n_j \hat{H}_j(v_q) \qquad \text{(XII; 6)}$$

It is to be stressed again that *all contingency information estimates* are composed linearly from certain *gain of information estimates.* (This important point is practically missed in the ecological literature, because of the lack of *systematic* treatment, and strange "potpourism" with "indeces" and names, where simple entropy estimates are frequently called "total information content" and similar rubish nicknames.) We might guess that the sum of the corresponding *lower* deviates play a similar role in composing another relevant information estimate. Indeed,

$$\left.\begin{aligned} \nabla N_j \hat{H}_j(V_q) + n_j \hat{H}_j(v_q) = ms\hat{H}_j([t, i] \mid q) - \\ - ms\hat{H}_j(t \mid [q, i]) - ms\hat{H}_j(i \mid [q, t]) = \\ = sm \log m - \alpha_j = ms\hat{I}_j([t, i] \mid q). \end{aligned}\right\} \qquad \text{(XIII; 7)}$$

(XIII; 7) is *a partial information function* referring to information of partners t and i, if q is neglected (or, say, in an experimental situation, if q is held *constant*).

XIII.4.2 We can see at once that there exists a simple additive relation between (XIII; 5) and (XIII; 7),

$$\left.\begin{aligned} ms\hat{I}_j(q, i) + ms\hat{I}_j([t, i] \mid q) = \\ = ms \log ms - \gamma_j = ms\hat{I}_j(i, [t, q]), \end{aligned}\right\} \qquad \text{(XIII; 8)}$$

where $ms\hat{I}_j(i, [t, q])$ is *a multiple information estimate* of partner i, with respect to the pair of other partners. It is obvious that

$$ms\hat{I}_j(i, [t, q]) = \Delta N_j \hat{H}_j(V_q) + \ldots + \nabla n_j \hat{H}_j(v_q), \qquad \text{(XIII; 9)}$$

i.e. (XIII; 8) is the sum of all the four *local* deviates. The main question is how can one interpret (XIII; 8) from the point of view of vegetation science.

XIII.4.3 A primary explanation should start with the statement that both (XIII.5) and (XIII; 7) are bounded in such a way that

$$\left.\begin{aligned} 0 \leq ms\hat{I}_j(q, i) \quad \leq msI_j(i, [q, t]), \\ 0 \leq msI_j([t, i] \mid q) \leq msI_j(i, [q, t]). \end{aligned}\right\} \qquad \text{(XIII; 10)}$$

Secondly, because of the composition of both information estimates of proper *local* deviates, we might guess tha $ms\hat{I}_j(q, i)$ approaches its upper bound if

K_j approaches an L-state, and $ms\hat{I}_j([t, i] \mid q)$ has an opposite "trend". For the sake of illustration, let us consider the local valence and invalence values of two simple cases, where $s = 4$, $m = 8$, and where ⟨A⟩ and ⟨B⟩ represents an l-state and an L-state, respectively.

⟨A⟩		⟨B⟩	
4	4	8	0
4	4	8	0
4	4	0	8
4	4	0	8
16	16	16	16

(XIII; 11)

Very simple calculation shows that

		⟨A⟩	⟨B⟩
(1)	$ms\hat{I}_j(q, i)$	0	32
(2)	$+ms\hat{I}_j([t, i] \mid q)$	32	0
(3)	$msI_j(i, [q, t])$	32	32

(XIII; 12)

i.e. (1) and (2) has its maximum value in an L-state and an l-state, respectively, within the interval permitted by (3). This kind of complementary relation is shown by data of (IX; 2) as well, where (1) 3.295 + (2) 28.617 = (3) 31.912.

XIII.4.4 If elements of a Q are labelled alphabetically such as $Q = \{a, b, c, \ldots\}$, and *the particular* (elementary) *finite schemes* are labelled by capital letters, $A = \{a, \bar{a}\}$, $B = \{b, \bar{b}\}$, ..., then we can denote $m\hat{H}_j(A)$, $m\hat{H}_j(B)$, ..., *particular local entropy functions* (in brief, *local entropy*), related to each element of Q. It is noteworthy that

$$m\hat{H}_j(A) + \ldots + m\hat{H}_j(S) = m\hat{H}_j([L]) = ms\hat{I}_i([t, i] \mid q), \quad \text{(XIII; 13)}$$

where $mH_j([L])$, *pooled local entropy*, equivalent to partial information estimate $ms\hat{I}_j([t, i] \mid q)$, is called by JUHÁSZ-NAGY and PODANI (1983) *local distinctiveness*. [For simple data of (IX; 2), $mH_j([L]) = 8 + 6.4906 + 7.6358 + 6.4906 = 28.617$.] According to (IX; 13), *associatum* is given by a relation which in itself is a good illustration of a better understanding of *attribute duality*; in words, associatum is equal to *local* distinctiveness minus *floral* entropy. [For data of (IX; 2), $m\hat{I}_j(\lambda) = 28.617 - 19.245 = 9.362$.] The meaning of local distinctiveness, however, is linearly complementary to that of $ms\hat{I}_j(q, i)$ which might be called *local evenness*. Both functions are meaningful only with respect to $ms\hat{I}_j(i, [q, t])$, *floristic insaturation*. Because γ_j is a biased U-shaped estimator (along the scale), floristic insaturation has a reversed U-shaped curve, with a local maximum at A_{comp}, compensatory area (where

$N_j \approx n_j$). and with a global minimum at $A_{\min}$ (if it exists). Note that approaching $A_{\min}$, all these functions tend to zero.

XIII.5 The arguments used in XIII.4 can safely be transferred into *floral relations*, gaining

$$\begin{array}{ll} (1) & msI_j(t, i) = sm \log m \; + \beta_j - \gamma_j \\ (2) & +msI_j([q, i] \mid t) = ms \log s \; - \beta_j \\ \hline (3) & msI_j(i, [q, t]) = ms \log ms - \gamma_j \end{array} \qquad \text{(XIII; 14)}$$

where (1) is *floral evenness*, (2) is *floral distinctiveness*, and (3) is again *floristic insaturation*. (1) is composed linearly as $\Delta N_j \hat{H}_j(V_t) + \Delta n_j \hat{H}_j(v_t)$, (2) can be composed either as $\nabla N_j \hat{H}_j(V_t) + \nabla n_j \hat{H}_j(v_t)$, or as *a pooled floral entropy estimate*, $s\hat{H}_j([F])$, analogous to (XIII; 13).

XIII.6 It is relevant to introduce at least two further information estimates, namely,

$$msI_j([q, t] \mid i) = ms\hat{H}_j([q, t] \mid i) - ms\hat{H}_j(q \mid [t, i]) - ms\hat{H}_j(t \mid [q, i]) =$$
$$= \gamma_j - \alpha_j - \beta_j, \qquad \text{(XIII; 15)}$$

and

$$msI_j([q, t, i]) = ms\hat{H}_j([q, t, i]) - ms\hat{H}_j(q \mid [t, i]) -$$
$$- ms\hat{H}_j(t \mid [q, i]) - ms\hat{H}_j(i \mid [q, t]) =$$
$$= ms \log ms - \alpha_j - \beta_j. \qquad \text{(XIII; 16)}$$

(XIII; 15) is *a partial information estimate* of partners q and t, with respect to partner i. In this case, the meaning of (XIII; 15) has the good interpretation of a contingency information estimate for q and t, if condition labelled by i is excluded, or, if i is held constant. Note that although $msI(q, t) = 0$, $msI_j([q, t] \mid i) \neq 0$, except special conditions (e.g. at $A_{\min}$). (XIII; 16) is *the joint information* for our trio of partners. This quantity should be kept clearly distinct from $msI_j(\langle q; t; i \rangle) = \alpha_j + \beta_j - \gamma_j$ which estimate (as $[msH(q) \cap \cap msH(t) \cap msH_j(i)]$) is distinguished in the terminology of GARDNER (1962) as *strictly defined interaction*. We might call (XIII.15) and XIII; 16) *floristic efficiency* and *floristic interaction*, respectively.

XIII.6.1 By using (XIII; 15) and (XIII; 16), some new additive relations can be gained, e.g.

$$\left.\begin{array}{l|l} msI_j(q, i) & \text{local evenness} \\ +msI_j([q, t] \mid i) & \text{floristic efficiency} \\ \hline msI_j([q, i] \mid t) & \text{floral distinctiveness} \end{array}\right\} \qquad \text{(XIII; 17)}$$

and

$$\left.\begin{array}{l|l} ms\hat{I}_j(t, i) & \text{floral evenness} \\ +ms\hat{I}_j([q, t] \mid i) & \text{floristic efficiency} \\ \hline ms\hat{I}_j([t, i] \mid q) & \text{local distinctiveness} \end{array}\right\} \qquad \text{(XIII; 18)}$$

XIII.6.2 (XIII; 17) and (XIII; 18) illustrate again the main point of IX.3.2, showing how can one gain some *floral* inference from some *local* quantities (and *vice versa*) *via* some proper *floristic* estimate. The same is true for (XIII; 19),

$$\left.\begin{array}{l|l} ms\hat{I}_j([t, i] \mid q) & \text{local distinctiveness} \\ +ms\hat{I}_j([q, i] \mid t) & \text{floral distinctiveness} \\ \hline ms\hat{I}_j([q, t, i]) & \text{floristic interaction} \end{array}\right\} \qquad \text{(XIII; 19)}$$

where the equality holds, even if (XIII; 19) implies only the sum of two *partial* estimates, because in this primitive system of models (as a consequence of our probability field is being a *classical* one) several different quantities may have the same value, e.g. $ms\widehat{H}_j(i \mid q) = ms\hat{I}_j(t, [q, i]) = ms\hat{I}_j([t, i] \mid q) = sm \log m - \alpha_j$. (Similar correspondences have been already taken into account.) Floristic estimates, of course, have their own reference with respect to each other, e.g.

$$\left.\begin{array}{l|l} ms\hat{I}_j([q, t] \mid i) & \text{floristic efficiency} \\ +ms\hat{I}_j(i, [q, t]) & \text{floristic insaturation} \\ \hline ms\hat{I}_j([q, t, i]) & \text{floristic interaction} \end{array}\right\} \qquad \text{(XIII; 20)}$$

XIII.7 Without going any further into some important details of the three partners modelling, let us consider some *close relations* between *associatum* and certain *estimates* treated above. Suppose we are interested here in the boundary relations of $m\hat{I}_j(\lambda)$.

XIII.7.1 Starting with *f*-marginals (viz. marginal idealizations), it is not too difficult to see that

(1) if a K_j is in an F-l-state, then $m\hat{I}_j(\lambda) = 0$, because $sm \log m = \alpha_j$, and $m\widehat{H}_j^{(\varphi)} = 0$,

(2) if a K_j is in an L-state, then $m\hat{I}_j(\lambda) = ms\hat{I}_j(i, [q, t]) - m\widehat{H}_j^{(\varphi)}$,

(3) if, in addition, an L-state is an f-L state, then, since $m\widehat{H}_j^{(\varphi)} = m\hat{I}_j(i, [q, t])$, $m\hat{I}_j(\lambda) = (s-1)m\hat{I}_j(i, [t, q]) = (s-1)mH_j^{(\varphi)}$,

(4) and, if our f-L-state occurs at A_{comp}, then $m\widehat{H}_j^{(\varphi)} = m$, and $m\hat{I}_j(\lambda) = (s-1)m$, which is the *global maximum* of associatum.

XIII.7.2 In a more realistic sense (i.e. in *a topologically "local" sense* with respect to the scale),

$$\max \hat{I}_j(\lambda) = m\bar{I}_j(\lambda) = ms\hat{I}_j(i, [q, t]) - m\widehat{H}_j^{(\varphi)}, \qquad \text{(XIII; 21)}$$

and, therefore,

$$m\bar{I}_j(\lambda) - m\hat{I}_j(\lambda) = ms\hat{I}_j(q, i), \qquad \text{(XIII; 22)}$$

that is, the difference between the *maximal* and *actual* values of associatum is equal to *local evenness*. (In other words, local evenness indicates the "*niveau-interval*" within which associatum can move.)

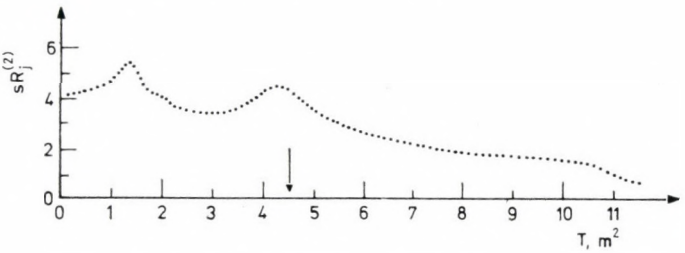

Fig. 6. An $sR_j^{(2)}(\lambda)$ *versus* T curve (see XIII.7)

XIII.7.3 According to (XIII; 22), it is plausible to introduce (XIII; 23), *a redundancy estimate*,

$$\widehat{sR}_j^{(2)}(\lambda) = 1 - m\hat{I}_j(\lambda)/ms\hat{I}_j(q, i), \qquad \text{(XIII; 23)}$$

in order to characterize a better *relative associatum* than (X; 1). Fig. 6 shows the curve of (XIII; 23) for the same object as fig. 4 does. The present curve is in many respects similar to that of fig. 4, but the second peak has a transformation toward $A_{\min}$ which property might make (XIII; 23) more "realistic" than (X; 1). For instance, the position of this second peak is quite close to the point, indicated in fig. 6, where the pooled positive association has its maximum.

XIII.8 A short comment is needed (at least, in the form of a few allusions to be developed later on) to call attention to some important relations between *equivalence analysis* and *three partners modelling*.

XIII.8.1 One of the key estimates is $ms\hat{I}_j([q, t] \mid i)$, *floristic efficiency*. It is easy to recognize that if a K_j is well-ordered, then

$$\left.\begin{aligned} N_j\hat{I}_j(E) + n_j\hat{I}_j(e) = ms\hat{I}_j(\varepsilon) = \\ = \gamma_j - \alpha_j - (\varepsilon_j - \delta_j) = msI_j([q, t] \mid i), \end{aligned}\right\} \qquad \text{(XIII; 24)}$$

because $(\varepsilon_j - \delta_j) = N_j\widehat{H}_j(V_q \mid V_R) + n_j\widehat{H}_j(v_q \mid v_r) = \beta_j$. Since the equation

$$\left.\begin{aligned} N_j\hat{I}_j(K) + n_j\hat{I}_j(k) = ms\hat{I}_j(X) = \\ = \gamma_j - \alpha_j - \beta_j = ms\hat{I}_j([q, t] \mid i) \end{aligned}\right\} \qquad \text{(XIII; 25)}$$

is satisfied for any K_j, if a K_j is not ordered, then the joint estimate

$$\hat{Y}_j + \hat{y}_j = \hat{\eta}_j = \varepsilon_j - \delta_j - \beta_j \qquad \text{(XIII; 26)}$$

is to be taken into account.

XIII.8.2 This has the consequence that a number of equations of this chapter can be rewritten in a suitable form, e.g.

$$ms\hat{I}_j([q, i] \mid t) = ms \log s - (\varepsilon_j - \delta_j) + \hat{\eta}_j, \qquad \text{(XIII; 27)}$$

which relates floral distinctiveness to some degree of orderliness. If K_j approaches orderliness, then $(\varepsilon_j - \delta_j) \to \beta_j$, and, $\hat{\eta}_j \to 0$.

XIV. Two partners modelling

XIV.1 Suppose that, contrary to the reasoning of XIII.1, partner i is neglected on the whole, and only partner q and t are regarded as "*true partners*", in exactly the same way as before (e.g. assuming classical probability field). These two partners are characterized at the first instant by f-marginals. (This kind of argument is perhaps "fitting" better to the traditional thinking of the "trade" than XIII.) It should be recognized, however, that we have already used (say, in an implicit form) *two kinds of two partners modelling*, associated with $N_j\hat{I}_j(E)$ and $N_j\hat{I}_j(K)$. Therefore, the present task is to make relevant relations more explicit, and try to show the proper interconnections between these constructions.

XIV.2 First of all, it is necessary to reconsider *coincidence information*, $N_j\hat{I}_j(K)$, and *incoincidence information*, $n_j\hat{I}_j(k)$, more closely, with particular reference to *extremal values* and *boundary relations*.

XIV.2.1 If joint entropy, $N_j\widehat{H}_j([V_q\ V_t]) = C_j - 0 = C_j$, is introduced, and $N_j\widehat{H}_j(V_q)$, $N_j\widehat{H}_j(V_t)$ are regarded as "familiar quantities" (see XII.1), then $N_j\hat{I}_j(K)$ can be redefined such as

$$\left.\begin{aligned} N_jH_j(V_q) + N_jH_j(V_t) - N_jH_j([V_q, V_t]) = \\ = C_j - A_j - B_j, \end{aligned}\right\} \qquad \text{(XIV; 1)}$$

with $N_j\widehat{H}_j(V_q \mid V_t) = B_j$, and $N_j\widehat{H}_j(V_t \mid V_q) = A_j$. *Mutatis mutandis*, similar relations are true for $n_j\hat{I}_j(k)$ as well.

XIV.2.2 If K_j is in an L-f-state, then $N_j\widehat{H}_j(V_q \mid V_t) = N_j \log \bar{s}_j$, $N_j\widehat{H}_j(V_t \mid V_q) = N_j \log m$, and, consequently, $N_j\hat{I}_j(K) = 0$. If K_j is either in a single f-state, or in a single l-state, without being in an oligovalence state on the part of the other type of marginals (like in the case of an [IRC]), then both $N_j\hat{I}_j(K)$ and $n_j\hat{I}_j(k)$ are greater than zero. If K_j is in an f-l-state, then

$N_j\hat{H}_j(V_q \mid V_t) = N_j \log \bar{s}_j$, $N_j\hat{H}_j(V_t \mid V_q) = N_j \log \bar{m}_j$, and so coincidence information has its *maximum*, $N_j\bar{I}_j(K)$,

$$N_j\bar{I}_j(K) = N_j \log \bar{N}_j \qquad \text{(XIV; 2)}$$

where $\bar{N}_j = ms/N_j$ (mean *total densiy* for coincidences), and, consequently, the same is true for incoincidence information,

$$n_j\bar{I}_j(k) = n_j \log \bar{n}_j, \qquad \text{(XIV; 3)}$$

where $\bar{n}_j = ms/n_j$ (mean *total density* for incoincidences).

XIV.2 For interpreting the pairwise bound,

$$\left.\begin{aligned} 0 \leq N_j\hat{I}_j(K) &\leq N_j\bar{I}_j(K) \\ 0 \leq n_j\hat{I}_j(k) &\leq n_j\bar{I}_j(k) \end{aligned}\right\} \qquad \text{(XIV; 4)}$$

both the equations of (XIV; 5) and (XIV; 6),

$$\left.\begin{aligned} &\Delta N_j\hat{H}_j\,(V_q) + \nabla N_j\hat{H}_j\,(V_q) = \\ &= \Delta N_j\hat{H}_j\,(V_t) + \nabla N_h\hat{H}_j\,(V_t) = N_j\bar{I}_j(K), \end{aligned}\right\} \qquad \text{(XIV; 5)}$$

$$\left.\begin{aligned} &\Delta n_j\hat{H}_j\,(v_q) + \nabla n_j\hat{H}_j\,(v_q) = \\ &= \Delta n_j\hat{H}_j\,(v_t) + \nabla n_j\hat{H}_j\,(v_t) = n_j\bar{I}_j(k), \end{aligned}\right\} \qquad \text{(XIV; 6)}$$

and the additive relation of (XIV; 7),

$$\left.\begin{aligned} N_j\hat{I}_j(K) + n_j\bar{I}_j(k) &= ms\bar{I}_j(X) = \\ &= ms\hat{I}_j(i, [q, t]), \end{aligned}\right\} \qquad \text{(XIV; 7)}$$

can be taken into account. (XIII; 25) and (XIV; 7) show clearly that in the present case there exist similar subdivisions, composed of the same estimates (namely, *f-deviates* of XII.), than in (XIII; 8), or in (XIII; 14). Further, by virtue of (XIII; 20), (XIII; 25), and (XIV; 7), we can see the intimate relations between three and two partners modellings, for instance, in the form of (XIV; 8),

$$\left.\begin{aligned} N_j\hat{I}_j(K) + n_j\hat{I}_j(k) + ms\hat{I}_j(i, [q, t]) &= \\ = ms\hat{I}_j([q, t, i]), \end{aligned}\right\} \qquad \text{(XIV; 8)}$$

where, in essence, we have the same subdivision than in (XIII; 20). If we define two special gain of information estimates of the second order,

$$\left.\begin{aligned} \Delta N_j\hat{I}_j(K) &= N_j\bar{I}_j(K) - N_j\hat{I}_j(K) \\ \Delta n_j\hat{I}_j(k) &= n_j\bar{I}_j(K) - n_j\hat{I}_j(k) \end{aligned}\right\} \qquad \text{(XIV; 9)}$$

then it is to be recognized that

$$\Delta N_j \hat{I}_j(K) + \Delta n_j \hat{I}_j(k) - ms\hat{I}_j(i, [q, t]) = ms\hat{I}_j(\langle q; t; i\rangle), \quad \text{(XIV; 10)}$$

where $ms\hat{I}_j(\langle q; t; i\rangle) = \alpha_j + \beta_j - \gamma_j$, strictly defined *interaction*, mentioned in XIII.6. (XIV; 10) means that the broadly and strictly defined interactions play central role in interpreting *f-marginal states* by means of two partners modelling.

XIV.3 In order to understand $N_j \hat{I}_j(E)$ even better than in part 1, or in XI., we can use the results of III. and XIV.2 for *another revision of equivalence information.*

XIV.3.1 Starting with the well-known equations of (XIV; 11),

$$\left.\begin{aligned} N_i \hat{I}_j(E) &= N_j \hat{I}_j(K) - \hat{Y}_j, \\ \hat{Y}_j = E_j - D_j - B_j &= N_j \hat{H}_j(V_q \mid V_R) - B_j, \end{aligned}\right\} \quad \text{(XIV; 11)}$$

it is to be recognized that *subcoincidence information*, $\hat{Y}_j$, can be regarded *by definition* as the sum in (XIV; 12),

$$\hat{Y}_j = \hat{y}_{j0} + \hat{y}_{j1} + \ldots + \hat{y}_{jr} + \ldots + \hat{y}_{js}, \quad \text{(XIV; 12)}$$

where the values of the multiplet variable R, $R = 0, 1, \ldots, s$, are implied in members of (XIV; 12) as indexing numbers at t_j (see III.). Note that $\hat{y}_{j0} = \hat{y}_{js} = 0$, for any [ET], because $\binom{s}{0} = \binom{s}{s} = 1$. If we have, for instance, an [IRC], where, as in (V; 8), $s = 4$, $m = s^s = 16$, then we can set up easily the three non-zero valued *subcontingency tables*, like (III; 3), such as

$(R = 1)$

1	0	0	0	1
0	1	0	0	1
0	0	1	0	1
0	0	0	1	1
1	1	1	1	4

$(R = 2)$

1	1	1	0	0	0	3
1	0	0	1	1	0	3
0	1	0	1	0	1	3
0	0	1	0	1	1	3
2	2	2	2	2	2	12

$(R = 3)$

1	1	1	0	3
1	1	0	1	3
1	0	1	1	3
0	1	1	1	3
3	3	3	3	12

(XIV; 13)

for which $Y_j = 8 + 12 + 4.9812 = 24.9812$. Let us call one table in (XIV; 3), or any such table in a similar series of tables, *an elementary contingency subtable*, [EST], and try to understand relations of (IX; 11) on the basis of (XIV; 12) by means of (XIV; 13).

XIV.3.2 It is fairly easy to conceive that for (XIV; 13), or, even for any [IRC], the pair of estimates, $\hat{Y}_j = \overline{Y}_j$, $\hat{y}_j = \overline{y}_j$, are of *maximum* values, because *any* [*EST*] *is in a double monovalence state*, and this *interlocal property* of an [ET] is responsible for such relations as $N_j \hat{I}_j(K) - \overline{Y}_j = N_j \hat{I}_j(E) = 0$, $n_j \hat{I}_j(k) - \overline{y}_j = n_j \hat{I}_j(e) = 0$. Generally speaking, and using the notation of

(III; 4), for any [EST] of an [IRC], where $0 < r < s$, the conditions of (XIV; 14)

$$\begin{array}{c|l} & \left.\begin{array}{l} r\ g_{jr}/s \\ \cdot \\ \cdot \\ \cdot \\ r\ g_{jr}/s \end{array}\right\} s \\ \hline \underbrace{r \ldots\ldots r}_{g_{jr} = \binom{s}{r}} & r\ g_{jr} \end{array} \qquad \text{(XIV; 14)}$$

are always satisfied; thus, $\bar{y}_{jr}$, contingency information estimate for [EST] in (XIV; 14) can be expressed as

$$\bar{y}_{jr} = g_{jr} r \log (s/r), \qquad \text{(XIV; 15)}$$

and, therefore,

$$\left.\begin{aligned} \bar{Y}_j &= \sum_{r=1}^{r-1} g_{jr} r \log (s/r) = \\ &= N_j \log s - B_j = \nabla N_j \hat{H}_j(V_t)\,. \end{aligned}\right\} \qquad \text{(XIV; 16)}$$

For illustrating these extremely simple relations, we can write down the values of (XIV; 15) for (XIV; 13) in order, gaining $\hat{y}_{j1} = 4 \cdot 1 \log (4/1) = 8$, $\hat{y}_{j2} = 6 \cdot 2 \log (4 \cdot 2) = 12$, $\hat{y}_{j3} = 4 \cdot 3 \log (4/3) = 4.9812$, and so $\hat{\bar{Y}}_j = 24.9812$, as before.

XIV.3.3 Contrary to the conditions of XIV.3.2, if a K_j is interlocally well-ordered, i.e. if it represents an [IOC], then each [EST] is in *an oligovalence state*, like (XIV; 17),

$$\begin{array}{c|l} & \left.\begin{array}{l} g_{jr} \\ \cdot \\ \cdot \\ \cdot \\ g_{jr} \end{array}\right\} r \\ & \left.\begin{array}{l} 0 \\ \cdot \\ \cdot \\ \cdot \\ 0 \end{array}\right\} (s - r) \\ \hline \underbrace{r \ldots r}_{g_{jr}} & r\ g_{jr} \end{array} \qquad \text{(XIV; 17)}$$

and, therefore, $\hat{y}_{jr} = 0$, $\hat{Y}_j = 0$. There are, of course, certain cases, like in (XIV; 18),

u	1	0	0	0	0	0	0	0	1
v	0	1	0	0	1	1	1	1	5
w	0	0	1	0	1	1	1	1	5
z	0	0	0	1	1	1	1	1	5
	1	1	1	1	3	3	3	3	16

(XIV; 18)

where we have a mixture of (XIV; 14) and (XIV; 18), and, therefore, $\hat{Y}_j = 8$ for (XIV; 18). We can rightly suppose that a still better understanding of orderliness is possible with respect to these extreme cases.

XIV.4 Using reasoning of XIV.2, (XIV; 16) implies *the double bound*

$$\left.\begin{aligned} Y_j &\leq \nabla N_j \hat{H}_j(V_t), \\ \hat{\eta}_j &\leq msI_j([q, i] \mid t), \end{aligned}\right\} \qquad \text{(XIV; 19)}$$

which shows how equivalence analysis is related to both three partners and two partners modellings. If a K_j is in an [IRC], then the upper bound of (XIV; 19) is satisfied which means that floral distinctiveness of (XIII; 27) is uniquely defined by $\hat{\eta}_j$, that is, $\Delta N_j \hat{H}_j(V_t) + \Delta n_j \hat{H}_j(v_t) = \hat{\eta}_j = ms\hat{I}_j(X) = msI_j([q, t] \mid i)$. If a K_j in an [IOC], then $\hat{Y}_j$ and $\hat{\eta}_j$ disappear, and, therefore, $ms\hat{I}_j(\varepsilon)$ is uniquely defined by $ms\hat{I}_j(X)$, and, by relations of (XIV; 10).

XIV.5 Of course, we might be interested in the problem of how orderliness of some kind is composed of some *elementary relations* (e.g. $q_i \in Q$), or, of some *coalitional relations* (e.g. $Q_k \subset Q$). This problem leads us to the family of diacretic models whose certain implications and importance will be discussed later on (see XVII.).

[C] SOME DIACRETIC MODELS

XV. Decomposition of associatum

XV.1 If we would like to study the populations one by one without "loosing the common touch" (and, roughly speaking, this is implied in the term "*dia*cretic modelling"), then a plausible way of doing this is shown by the following simple formalism.

XV.2 Starting with XIII.4.4, in particular, with (XIII.13), let us consider population "a". By letting

$$m\hat{H}_j(A \mid [B, C, \ldots, S]) = m\hat{H}_j(\{A\}), \qquad \text{(XV; 1)}$$

where

$$m\hat{H}_j(\{A\}) = m\hat{H}_j(A) - m\hat{I}_j(\langle A\rangle), \qquad \text{(XV; 2)}$$

where

$$m\hat{I}_j(\langle A\rangle) = m\hat{I}_j(A, [B, C, \ldots, S]) \qquad \text{(XV; 3)}$$

$$= m\hat{I}_j(\lambda) - m\hat{I}_j([\bar{A}]), \qquad \text{(XV; 4)}$$

and where

$$m\hat{I}_j([\bar{A}]) = m\hat{I}_j([B, C, \ldots, S]), \qquad \text{(XV; 5)}$$

it is possible to introduce the following decomposition (to be called more precisely, *an elementary decomposition*) of associatum, with respect to one single population, namely, "*a*":

(1)	$m\hat{H}_j(A)$	local entropy	
(2)	$-m\hat{H}_j(\{A\})$	complete dissociation	
(3)	$m\hat{I}_j(\langle A\rangle)$	complete association	(XV; 6)
(4)	$+m\hat{I}_j([\bar{A}])$	subassociatum	
(5)	$m\hat{I}_j(\lambda)$	associatum	

A similar decomposition is straightforward for all elements of Q.

XV.2.1 First, an explanation of terms is in order (see Fig. 6). (2) in (XV; 6) is *a multiple conditional entropy* estimate for "*a*" with respect to all other elements of Q. In other words, $m\hat{H}_j(\{A\})$ is a measurable subset of $m\hat{H}_j(A)$, local entropy, that is not "shared" by any other population. (Hence the name "*complete dissociation*" refers to the "unique interlocal behaviour" of the population concerned.) On the other hand, (3) in (XV; 6) is *complete association* of "*a*", because it is the measurable subset of $m\hat{H}_j(A)$ which is in *some* "interaction" with others, in the interlocal sense of the word (i.e. it is "shared" by at least one other population). (3), in the form of (XV; 3), is *a multiple information* estimate; that is, the difference of two closely related quantities, *associatum and subassociatum.*

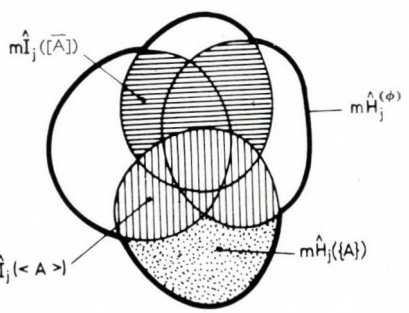

Fig. 7. Graphical explanation of model in XV. as a "measurable" VENN-diagram (see XV.2.1)

XV.2.2 Secondly, note that in the first part of (XV; 6), namely in (1)—(3), the main purpose of the construction is *to distinct* "*a*"; in the second part /(4)—(5)/ of it, a special kind of *elimination of* "*a*" is aimed at. The key concept of this elimination is *subassociatum*, related to $[\bar{A}]$, $[\bar{A}] = [B, C, \ldots, S]$, a joint scheme *not* containing "*a*". Therefore,

$$m\hat{I}_j([\bar{A}]) = m\hat{H}_j([L \mid A]) - m\hat{H}_j^{(\varphi|A)}, \qquad \text{(XV; 7)}$$

where $mH_j([L \mid A])$ is the pooled local entropy with the omission of "*a*"-data (local distinctiveness without "*a*"), and

$$m\hat{H}_j^{(\varphi|A)} = m\hat{H}_j([B, C, \ldots, S]), \qquad \text{(XV; 8)}$$

where $m\hat{H}_j^{(\varphi|A)}$ is *floral subdiversity* of an [ET], if local vector belonging to "*a*" is eliminated. In other words, subassociatum is joint (total) information of a $2 \times 2 \times \ldots^{s-1} \times 2$ table, instead of being a joint information estimate of a $2 \times 2 \times \ldots^{s} \times 2$ table.

XV.3 In a more detailed way,

$$\begin{aligned} m\hat{I}_j(\langle A \rangle) &= m\hat{I}_j(\lambda) - m\hat{I}_j([\bar{A}]) = \\ &= m\hat{H}_j([L]) - m\hat{H}_j^{(\varphi)} - m\hat{H}_j([L \mid A]) + m\hat{H}_j([\bar{A}]) = \\ &= \{m\hat{H}_j[L] - m\hat{H}_j([L \mid A])\} - \{m\hat{H}_j^{(\varphi)} - m\hat{H}_j([\bar{A}])\}, \end{aligned} \qquad \text{(XV; 9)}$$

where (XV; 9) is *a difference* of *two kinds* of *gain of information* estimates. The first member of (XV; 9) refers to *local quantities*, only; the second member of (XV; 9) reflects to *interlocal quantities*, which implies that

$$m\hat{H}_j(\{A\}) = m\hat{H}_j^{(\varphi)} - m\hat{H}_j([B, C, \ldots, S]). \qquad \text{(XV; 10)}$$

(XV; 10) is practically useful, because, in most cases, total dissociation can optimally estimated by means of subdiversity values. "*Subdiversity*", as a concept, has a special interest of its own; the present meaning is simple, because of the combinatorial interpretation of $m\hat{H}_j^{(\varphi)}$.

XV.4 Due to the meaning of terms in (XV; 6), it is possible to introduce the concepts of *associativity* and *dissociativity* of population in the following sense of the words.

XV.4.1 It is plausible to state that (*a*) *associativity* of population "*a*" is of *maximum* value if and only if $m\hat{H}_j(\{A\}) = 0$, $m\hat{I}_j(\langle A \rangle) = m\hat{H}_j(A)$, and (*b*) associativity of "*a*" is of *minimum* value, if and only if $m\hat{I}_j(\langle A \rangle) = 0$, $m\hat{H}_j(\{A\}) = m\hat{H}_j(A)$.

XV.4.2 For reasons to be considered later on (see XVI.), it is better to follow another way of thinking of defining dissociativity. First, it is to be

noted that complete dissociation estimates for all elements of Q are "independent" from each other, and therefore, *additive*,

$$m\widehat{H}_j(\{A\}) + m\widehat{H}_j(\{B\}) + \ldots + m\widehat{H}_j(\{S\}) = m\widehat{H}_j\{\delta_\lambda^{(s)}\}, \quad \text{(XV; 11)}$$

where $m\widehat{H}_j\{\delta_\lambda^{(s)}\}$ is called *total dissociatum* of Q. (Total dissociatum is a measurable subset of $m\widehat{H}_j^{(\varphi)}$ which is excluded from all kinds of "interactions", i.e. manifested interlocal relations.) Secondly, by supposing that $m\widehat{H}_j\{\delta_\lambda^{(s)}\} > 0$, we can define for population "a"

$$\widehat{R}_j(\{A\}) = m\widehat{H}_j(\{A\})/m\widehat{H}_j\{\delta_\lambda^{(s)}\} \quad \text{(XV; 12)}$$

which redundancy estimate makes possible *to rank* populations according to their degrees of dissociativity ($0 \leq \widehat{R}_j(\{A\}) \leq 1$).

XV.5 For the sake of a primary illustration, let us consider an [ET] in (XV; 13), where $s = 3$, $m = 8$, $m\widehat{H}_j^{(\varphi)} = 16$, $m\hat{I}_j(\lambda) = 8$, $m\widehat{H}_j\{\delta_\lambda^{(s)}\} = 8$,

a	0	0	0	0	1	1	1	1	4
b	0	0	1	1	0	0	1	1	4
c	0	0	0	0	1	1	1	1	4
	0	0	1	1	2	2	3	3	12

(XV; 13)

The values of estimates (XV; 6) are shown by (XV; 14).

	a and *c*	*b*
(1)	8	8
(2)	−0	−8
(3)	8	0
(4)	+0	+8
(5)	8	8

(XIV; 14)

We can see at once that "*a*" and "*c*" have a maximum degree of associativity, and a minimum degree of dissociativity, while "*b*" has an opposite qualification (with maximum degree of dissociativity, and minimum degree of associativity). This observation is consistent with proper interlocal relations as well. Since the pairs (a, b) and (b, c) are stochastically independent, but the pair (a, c) is *not* independent (i.e. interlocally dependent), the special interlocal role of "*b*" is explained by the relation that "*b*" *is* element of both independent pairs, but it *is not* an element of the single dependent pair. This kind of simple reasoning can be applied to an [IRC], as (IX; 5), where, since all the possible pairs are independent, and therefore all elements have a maximum degree of dissociativity, and a minimum degree of associativity.

XV.5.1 Turning to a less trivial case, consider (IX; 2), where $s = 4$, $m = 8$, and where $m\widehat{H}_j^{(\varphi)} = 19.2453$, $m\hat{I}_j^{(\lambda)} = 9.3717$, $m\widehat{H}_{j\{\lambda}^{\{(4)}\delta\}} = 10.3263$. The estimates of (XV; 6) for (IX; 2) is shown by (XV; 15):

	u	v	w	z
(1)	8.0000	6.4906	7.6358	6.4906
(2)	−3.2353	−0.0000	−3.2453	−4.0000
(3)	4.7547	6.4906	4.3905	2.4906
(4)	+4.6170	+2.8811	+4.9812	+6.8811
(5)	9.3717	9.3717	9.3717	9.3717

(XV; 15)

According to (XV; 15), (*a*) *the associativity ranking* of elements in (IX; 2) is: $v > u > w > z$; while (*b*) *the dissociativity ranking* of these elements is: $z > | u \sim w | > v$. Note that (*a*) is not related trivially to (*b*), *et vice versa*; for instance, we cannot explain, without further considerations, why the tie "$u \sim w$" exists in (*b*), or, why v has in (XV; 15) its zero-valued complete dissociation. Note, further, that the values of total dissociation can easily be estimated by (XV.10), as it is shown by (XV; 16),

	u	v	w	z
$\langle 1 \rangle$	19.2453	19.2453	19.2453	19.2453
$-\langle 2 \rangle$	16.0000	19.2453	16.0000	15.2453
$\langle 3 \rangle$	3.2453	0.0000	3.2453	4.0000

(XV; 16)

where $\langle 1 \rangle$ is floral diversity, $\langle 2 \rangle$ is floral subdiversity, and $\langle 3 \rangle$ is total dissociation.

XV.5.2 Ranking procedures are fairly important in understanding of how elements are related to each other (see ORLÓCI 1978b). There are, however, different types ranking, and simple "cumulative ranks" (i.e. ranks by means of pooled information estimates) might be rather misleading in several cases.

XVI. Notes on further modelling

XVI.1 Clearly, (XV; 6) represents an *elementary* decomposition of associatum, because this simple additive model refers to one single element of Q, $q_i \in Q$, only. Suppose that we would like to generalize the reasoning of XV., in order to cover *coalitional relations* (or, speaking in more traditional terms, "group relations") of a Q as well, related to some Q_k coalition of Q, $Q_k \subset Q$. This intention is justitiable for a number of good motives. For instance, this kind of generalization opens up some new possibilities to a better interconnection of synmorphology and syntaxonomy (say, clustering methods) in the fu-

ture. Similarly, if we were able to attach analogous estimates to coalitions (and, say, to rank these coalitions according to their complete association or dissociation of some kinds), then our knowledge would be more advanced as to the "collective structural relations" of the communities.

XVI.2 The first obstacle of making such generalizations is that $m\hat{H}_j^{(\varphi)} \neq$ $\neq m\hat{I}_j(\lambda) + m\hat{H}_j\{\delta_\lambda^{(s)}\}$, because of the existence of "multiple overlaps". Taking again the simple example of (IX; 2), where $m\hat{H}_j^{(\varphi)} = 19.2453$, $m\hat{I}_j(\lambda) =$ $= 9.3717$, $m\hat{H}\{\delta_\lambda^{(4)}\} = 10.3263$, the inequality indicated before is due to a quantity, 0.453 in value, which is to be called "*interassociatum*" in this chapter. Interassociatum may be, in a number of cases, of small value that can be occasionally neglected. This negligence, however, should be an *a posteriori* operation; *a priori*, it is at least to be clarified what is to be meant by interassociatum. Our present aim cannot go any further than to study briefly some relevant estimates and basic relations whose better understanding and usage will be treated in some next parts of this series of papers (or, elsewhere).

XVI.3 Suppose that, in analyzing an [ET], we distinguish some multiplets, say, *v-test of elements*. Suppose, further, that we confine here our attention to *local v-tets*, $2 \leq v \leq (s-1)$. A local multiplet of v order can be studied by means of *an interlocal scheme* of the same order; the best known example is a set of 2×2 table, if $v = 2$. If we want to generalize the traditional "pairwise reasoning" of association analysis to any v, then we have to introduce a general notation.

XVI.3.1 Let $m\hat{H}_j\{\Sigma_\lambda^{(v)}\}$ be *the pooled interlocal entropy estimate* of the v-order, i.e. for the whole set of the joint schemes of the v-order. Let $m\hat{I}_j\{\Sigma_\lambda^{(v)}\}$ be corresponding *pooled information estimate* of the same order such as

$$m\hat{I}_j\{\Sigma_\lambda^{(v)}\} = \binom{s-1}{v-1}[sm \log m - \alpha_j] - m\hat{H}_j\{\Sigma_\lambda^{(v)}\} = \\ = \binom{s-1}{v-1} ms\hat{I}_j([t, i] \mid q) - m\hat{H}_j\{\Sigma_\lambda^{(v)}\}, \qquad \text{(XVI; 1)}$$

where $ms\hat{I}_j([t, i] \mid q)$ is again *local distinctiveness* (see XIII.4).

XVI.3.2 In order to illustrate (XVI; 1), let us turn again to (IX; 2), where $ms\hat{I}_j([t, i] \mid q) = 28.617$, $m\hat{H}_j\{\Sigma_\lambda^{(2)}\} = 76.0263$, $m\hat{H}_j\{\Sigma_\lambda^{(3)}\} = 66.4906$, and thus

$$\left.\begin{aligned} m\hat{I}\{\Sigma_\lambda^{(2)}\} &= \binom{3}{1} 28.617 - 76.0263 = \ 9.8247, \\ m\hat{I}_j\{\Sigma_\lambda^{(3)}\} &= \binom{3}{2} 28.617 - 66.4906 = 19.3604. \end{aligned}\right\} \qquad \text{(XVI; 2)}$$

The sums gained in (XVI; 2) have to correspond to the sums of proper interlocal association estimates, e.g. $m\hat{I}_j\{\Sigma_\lambda^{(2)}\} = m\hat{I}_j([U, V]) + \ldots + m\hat{I}_j([W, Z]$ where $m\hat{I}_j([U, V]) = 2.4906$, $m\hat{I}_j([W, Z]) = 0.1264$. By listing information estimates for triplets, $m\hat{I}_j([U, V, W]) = 6.8811$, $m\hat{I}_j([U, V, Z]) = 4.9812$, $m\hat{I}_j([U, W, Z]) = 2.8811$, $m\hat{I}_j([V, W, Z]) = 4.617$, and by adding these values, we gain again the sum 19.3604, as in (XVI; 2).

XVI.3.3 Having these primary pooled quantities, we can estimate *interassociatum of the* (v + 1) *order* such as

$$mI_j([\lambda_{(v+1)}]) = \left[\binom{s-1}{v-1} - (v-1)\right] ms\hat{I}_j([t, i] \mid q) - m\widehat{H}_j\{\Sigma_\lambda^{(v)}\} + \\ + (v-1)\, m\widehat{H}_j^{(q)} = m\hat{I}_j\{\Sigma_\lambda^{(v)}\} - (v-1)\, m\hat{I}_j(\lambda) \qquad \text{(XVI; 3)}$$

For instance, (XVI; 3) has the pair of values for our data of XVI.3.2,

$$\left.\begin{aligned} m\hat{I}\acute{\imath}([\lambda_{(4)}]) &= 19.3604 - 18.7434 = 0.617, \\ m\hat{I}\acute{\imath}([\lambda_{(3)}]) &= 9.8247 - 9.3717 = 0.453. \end{aligned}\right\} \qquad \text{(XVI; 4)}$$

XVI.3.4 The meaning of interassociatum of some order corresponds to *multiple interaction*, exactly in the sense of KULLBACK (1959). Speaking perhaps in more picturesque terms, interassociatum measures *the multiple overlaps* of local entropy estimates of an [ET] at a given order. As KULLBACK explains it properly, such interaction terms may be *of negative values*. The author has the experience that, during a secondary succession, the progress of degradation is frequently resulted in the increase of negative interassociatum estimates, sometimes for the majority of orders.

XVI.4 The concept of interassociatum is closely and complementarily related to that of *dissociatum*. The primary point is that if we do not consider *total dissociatum* (as in XVI.4.2), then, as in XVI.3, we should tackle dissociatum estimates of different orders.

XVI.4.1 Using the same reasoning and symbolism as before, *dissociatum of the* (v + 1) *order* can be estimated as

$$\left.\begin{aligned} m\widehat{H}_j\{\delta_\lambda^{(v+1)}\} = \left[\binom{s-1}{v-1} - v\right] ms\hat{I}_j([t, i] \mid q) - m\widehat{H}_j\{\Sigma_\lambda^{(v)}\} + \\ + (v+1) m\widehat{H}_j^{(q)} = ms\hat{I}_j([t, i] \mid q) - [(v+1) mI_j(\lambda) - m\hat{I}_j\{\Sigma_\lambda^{(v)}\}]. \end{aligned}\right\} \qquad \text{(XVI; 5)}$$

If $v = (s - 1)$, then (XVI; 5) is happily reduced to (XVI; 6),

$$m\widehat{H}_j\{\delta_\lambda^{(s)}\} = sm\widehat{H}_j^{(q)} - m\widehat{H}_j\{\Sigma_\lambda^{(s-1)}\}, \qquad \text{(XVI; 6)}$$

where total dissociatum can be regarded as a special kind of gain of information estimate. For data of (XI; 2), the value of (XVI; 6) can be given as $m\widehat{H}_j\{\delta_\lambda^{(4)}\} = = 4 \cdot 19.2453 - 66.4906 = 10.4906$, as before. Note that $sm\widehat{H}_j^{(\varphi)}$ in (XVI; 6) is specifically weighted floral diversity.

XVI.4.3 The main importance of dissociatum is shown by (XVI; 7),

$$m\widehat{H}_j^{(\varphi)} = mH_j\{\delta_\lambda^{(v+1)}\} + m\hat{I}_j(\lambda) - mI_j([\lambda_{(v+1)}]), \qquad \text{(XVI; 7)}$$

where we have a well-defined additive subdivision of floral diversity as an "overall uncertainty bound" for interlocal relations. The particular subdivisions for data of (IX; 2) are given by (XVI; 8),

$$\left.\begin{array}{ll} (v = 3) & 19.2453 = 10.4906 + 9.3717 - 0.617 \\ (v = 2) & 19.2453 = 10.3266 + 9.3717 - 0.453 \end{array}\right\} \qquad \text{(XVI; 8)}$$

As it has been stressed before, interaction terms (i.e. *interassociata*) might be neglected, if the particular values are small, but it is always relevant to know how such an additive composition is built up as (XVI; 7).

XVI.5 (XVI; 7), however, is by no means the only additive subdivision which can be constructed from our present, our closely related estimates. Some examples are given for further use.

XVI.5.1 By simple rearrangement of proper terms, it is obvious that

$$m\hat{I}_j([\lambda_{(v)}]) = m\widehat{H}_j^{(\varphi)} - m\widehat{H}_j\{\delta_\lambda^{(v+1)}\} \qquad \text{(XVI; 9)}$$

We may define a new estimate, called *manifest associatum*,

$$m\hat{I}_j\{\lambda_{(v)}\} = vm\hat{I}_j(\lambda) - m\hat{I}\{\Sigma_\lambda^{(v)}\} \qquad \text{(XVI; 10)}$$

which play a fairly important role in understanding of how associatum and interassociatum are related to each other. Using (XVI; 9) and (XVI; 10), we can obtain an interesting subdivision of $ms\hat{I}_j(i, [q, t])$, *floristic insaturation* (see XIII.4),

$$\begin{array}{l|l|l} ms\hat{I}_j(q, i & 3.2952 & \\ +m\hat{I}_j(\lambda) & 9.3717 & m\hat{I}_j(\langle\lambda\rangle) = 12.6669 \\ +m\hat{I}_j\{\lambda_{(3)}\} & 8.7547 & \\ +mH_j\{\delta_\lambda^{(4)}\} & 10.4906 & mH_j^{(\varphi)} = 19.2453 \\ \hline ms\hat{I}_j(i, [q, t]) & 31.9122 & \end{array} \qquad \text{(XVI; 11)}$$

where $m\hat{I}_j(\langle\lambda\rangle)$ is *hyperassociatum*, possible local maximum for given data.

XVI.5.2 By defining two new estimates,

$$ms\hat{I}_j([t, i] \mid q^{(v-1)}) = (v + 1)\, m\hat{I}_j(\lambda) - m\hat{I}_j\{\Sigma_\lambda^{(v)}\}, \qquad \text{(XVI; 12)}$$

called *manifest local distinctiveness* at a given order, and,

$$m\hat{I}_j\{\Pi_\lambda^{(v)}\} = m\hat{I}_j(\lambda) - (s-1)\, m\hat{I}_j([\lambda_{(v+1)}]), \qquad \text{(XVI; 13)}$$

called *local particulatum* at a given order, it is possible to introduce several other subdividions. A particularly important one is shown by (XVI; 14),

$$m\hat{I}_j\{\lambda_{(v)}\} = m\hat{I}_j\{\pi_\lambda^{(v)}\} + m\hat{I}_j([\lambda_{(v+1)}]) \qquad \text{(XVI; 14)}$$

which is a subdivision of manifest associatum into two component estimates, particulatum and interassociatum. The relevance of the concept "particulatum" is shown by the triple comparison:

— *dissociatum* indicates "*no interaction*"
— *particulatum* indicates "*partial interaction*"
— *interassociatum* indicates "*full interaction*"

at a given order and in a given context. In other words, particulatum is the measurable subset of $m\widehat{H}_j^{(q)}$ which is *not shared* by *all elements* of Q at a given order. Using these new estimates, we can produce another subdivision of floristic insaturation, similar to (XVI; 11),

$ms\hat{I}_j(q, i)$	3.2952		
$+m\hat{I}_j(\lambda)$	9.3717	$ms\hat{I}_j([t, i] \mid q^{(3)} = 18.1264$	(XVI; 15)
$+m\hat{I}_j\{\Pi_\lambda^{(3)}\}$	7.5207		
$+m\hat{I}_j\{\lambda_{(4)}\}$	1.2340		
$+m\hat{H}_j\{\delta_\lambda^{(4)}\}$	10.4906		
$ms\hat{I}_j(i, [q, t])$	31.9122		

XVI.6 Without listing further a number of interesting additive relations, let us turn back to our primary concern (XVI.1), i.e. possible coalitional subdivisions of relevant estimates.

XVI.6.1 First, it is to be noted that, having a number of new estimates, the pooled data of (XV; 15) make sense

(1)	$ms\hat{I}_j([t, i] \mid q)$	28.6170	
(2)	$-m\widehat{H}\{\delta_\lambda^{(s)}\}$	−10.4906	
(3)	$ms\hat{I}_j([t, i] \mid q^{(s-1)})$	18.1264	(XVI; 16)
(4)	$+m\hat{I}_j\{\Sigma_\lambda^{(s-1)}\}$	+19.3604	
(5)	$sm\hat{I}_j(\lambda)$	37.4868	

where, for instance, (3) is the proper manifest local distinctiveness, or, (4), sum of subassociatum estimates, appears in (XVI.16) as the pooled information estimates for triplets, as in (XVI; 2).

XVI.6.2 Suppose we are interested here in coalition Q_k, $Q_k \cap \bar{Q}_k = Q$. In a more complicated case, we have a partition of $Q, Q_1, Q_2, \ldots, Q_k, \ldots$, i.e. $\bigcup_k Q_k = Q$, $Q_j \cap Q_k = \emptyset$, $j \neq k$.) Then, *ad analogiam* of (XV; 6), we can set up (XVI; 17) for Q_k

(1)	$m\hat{H}_j([Q_k])$	coalitional entropy
(2)	$+m\hat{I}_j([Q_k])$	coalitional association
(3)	$m\hat{I}_j\{Q_k\}$	special distinctiveness
(4)	$-m\hat{H}_j(\Phi : Q_k)$	elimination entropy
(5)	$m\hat{I}_j(\langle Q_k \rangle)$	complete association
(6)	$+m\hat{I}_k([Q_k])$	subassociatum
(7)	$m\hat{I}_j(\lambda)$	associatum

(XVI; 17)

Special distinctiveness can be estimated as

$$m\hat{I}_j\{Q_k\} = km \log m - \alpha_j^{(k)}, \qquad \text{(XVI; 18)}$$

where $\alpha_j^{(k)}$, $\alpha_j^{(k)} < \alpha_j$, is the sum of local estimates of those elements that are elements of Q_k. *Elimination entropy*,

$$m\hat{H}_j(\Phi : Q_k) = m\hat{H}_j^{(\varphi)} - m\hat{H}_j([\bar{R}_k]), \qquad \text{(XVI; 19)}$$

can be regarded as a special kind of gain of information estimate, with respect to Q_k. (XVI; 20) gives a primary illustration of (XVI; 17), only for three pairs of elements, and using only the numbers of (XVI; 17):

	(u, v)	(u, w)	(v, w)
(1)	12.00	15.24	10.39
+(2)	2.49	0.39	3.73
(3)	14.49	15.63	14.12
−(4)	5.24	6.85	7.24
(5)	9.25	8.78	6.88
+(6)	0.12	0.59	2.49
(7)	9.37	9.37	9.37

(XVI; 20)

XVI.6.3 Fortunately enough, (XVI; 17) and (XVI; 20) are "redundant", because

$$\left.\begin{aligned} m\hat{I}_j(\lambda) &= m\hat{H}_j([Q_k]) + m\hat{H}_j([\bar{Q}_k]) - m\hat{H}_j^{(\varphi)} - m\hat{I}_j([Q_k]) - m\hat{I}_j([\bar{Q}_k]) = \\ &= m\hat{I}_j([Q_k], [Q_k]) + m\hat{I}_j([Q_k]) + m\hat{I}_j([\bar{Q}_k]), \end{aligned}\right\} \text{(XVI; 21)}$$

and, by (XVI; 21), the relations of (XVI; 17) are reduced to the form of (XVI; 22)

	(u, v)	(u, w)	(u, z)
$m\hat{I}_j([Q_k])$	2.4906	0.3905	2.4906
$+m\hat{I}_j([Q_k], [\bar{Q}_k])$	6.7547	8.3905	3.1452
$m\hat{I}_j(\langle Q_k \rangle)$	9.2453	8.7810	5.6358
$+m\hat{I}_j([\bar{Q}_k])$	0.1264	0.5907	3.7379
$m\hat{I}_j(\lambda)$	9.3717	9.3717	9.3717

(XVI; 22)

Note that because $m\hat{I}_j([Q_k], [\bar{Q}_k])$, *collective association*, is a symmetric quantity (since $Q_k \cup \bar{Q}_k$ is a symmetric relation in itself),

$$\left.\begin{aligned} m\hat{I}_j([Q_k], [\bar{Q}_k]) = m\hat{I}_j([\bar{Q}_k], [Q_k]) = \\ = m\hat{H}_j([Q_k]) + m\hat{H}_j([\bar{Q}_k]) - m\hat{H}_j^{(\varphi)}, \end{aligned}\right\} \qquad \text{(XVI; 23)}$$

(XVI; 22) is partly informative for the other three pairs as well. [This is why the pair (u, z) is chosen here, instead of (v, w), as in (XVI; 20).]

XVI.6.4 Note, further, that the sum of the collective association estimates is equal to the value of manifest local distinctiveness, i.e.

$$\left.\begin{aligned} sm\hat{I}_j([t, i] \mid q^{(2)}) + m\hat{I}_j\{\Sigma_\lambda^{(2)}\} = 3 \cdot m\hat{I}_j(\lambda) \\ 18.2904 \quad + 9.8247 \quad = 28.1151 \end{aligned}\right\} \qquad \text{(XVI; 24)}$$

which has the implication that

$$\left.\begin{aligned} 2 \cdot m\hat{I}_j(\lambda) - sm\hat{I}_j([t, i] \mid q^{(2)}) = m\hat{I}_j([\lambda_{(2)}]) \\ 18.7434 - \quad 18.2904 \quad = 0.453 \end{aligned}\right\} \qquad \text{(XVI; 25)}$$

as before.

XVII. Some interim remarks

XVII.1 These models can be useful in several ways. For instance, we might be interested in ranking coalitions, according to their *complete association*. (During a process of some kind, we should face, of course, the difficult problems of "trans-ranking".) This argument may lead us to redefine the old but still unsolved problems of "*dominance structures*" *of communities* (see MAY, 1981). It is perhaps not too far-fetched to believe that the most dominant, the second most dominant etc. elements or coalitions are not defined *only* by their abundance relations but, *prima facie*, by their "*associational powers*" by which they truly "dominate" over other elements or coalitions.

XVII.2 Let us make a distinction between (a) *autophenetic* and (b) *synphenetic patterns*. Concept (a) is related to one single element of a set, like the Bangorian "species pattern" representations. Concept (b) is related to all (or, at least, conventionally all) elements of a set, like a number of diversity pattern representations (see e.g. GREIG-SMITH 1964; PATIL and ROSENZWEIG 1979).

XVII.2.1 The efficient translation of (a) to (b), and *vice versa*, is still very limited. The aim of the present paper was to describe some tools to make this kind of communication, or, translation more efficient. The *syncretic* models of [B] and the *diacretic* models of [C] refer, of course, to *some synphenetic* and *autophenetic patterns*, respectively.

XVII.2.2 We should be aware of the fact that some seemingly simple problems are "classical" but somehow neglected. KYLIN, for instance, had made clear and operational distinction between the "minimiareals" of a species and a community (see GOODALL 1952). Instead of forgetting important results, it is much better to try to follow the tracks of our ancestors.

XVII.3 If we generalize the reasoning of KYLIN and others, then all concepts of X. (e.g. characteristic points, intervals, scaling, screening etc.) have to be interpreted for elements and coalitions as well. We might guess that there exist some empirically "good" (although probably not simple) relations between certain autophenetic and synphenetic parameters. For instance, in the the majority of cases there is an accumulation of particular maxima of complete dissociation for most populations around A_{diss}, the characteristic point, where total dissociatum reaches its maximal value. The detection of such "multi-pattern" relations can be made only by having a reasonably rich repertoir of models. The next parts of this series will keep this aim in view.

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ANALYSIS OF MAPPED AND SIMULATED VEGETATION PATTERNS BY MEANS OF COMPUTERIZED SAMPLING TECHNIQUES

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Three computer programs have been developed to perform simulated sampling based on mapped and digitized vegetation data. These programs are used in comparing simulated random patterns to real vegetation maps obtained in two different steppe communities, one from Hungary and the other from Canada. The relationships between sampling characteristics and information theoretical functions are analyzed. Possibilities for determining characteristic areas defined in terms of information theoretical functions and expected resemblance are also examined. In two simple situations it is tested whether overlap among sample plots and simplification in the representation of plant pattern strongly influence results obtained in sampling simulation experiments

Introduction

Mapped vegetation data have long been used in various fields of vegetation ecology to investigate spatial pattern, the efficiency of sampling designs and the interrelationship between population parameters. The usefulness of maps lies in the wide range of sampling techniques that can be implemented and compared automatically which would not be possible to do in a field survey. Further advantage is that artificial maps can be generated to test the performance of analytical methods. In case of point patterns, vegetation data can be easily transformed to coordinates and the whole procedure can be performed by computers. For these reasons, the applications of artificial and real maps to vegetation surveys are numerous (e.g., PENFOUND 1945, CURTIS and MCINTOSH 1950, GREIG-SMITH 1952, BORMANN 1953, COTTAM et al. 1957, O'REGAN and PALLEY 1965, O'REGAN et al. 1973, ARVANITIS and O'REGAN 1967, KULOW 1966, WILLIAMS et al. 1969, LAFRANCE 1972, NOSEK 1976, SZŐCS 1977, 1979, DIGGLE 1981, BONNICKSEN and STONE 1981) despite some disadvantages attributed to the method (e.g. edge effect, plant representation problems) discussed below.

The idea of computer simulated sampling applied to mapped vegetation emerged first in forest studies and is dated back as early as the sixties. PALLEY and O'REGAN (1961) described a technique for the evaluation of point and line sampling methods using the coordinates of individual plants stored in computer memory. Their program was modified later for sampling with circular plots (O'REGAN and PALLEY 1965). These techniques were widely used to find optimum sampling designs for estimating forest population parameters such as timber volume, basal area and frequency (ARVANITIS and O'REGAN 1967, WENSEL and JOHN 1969, O'REGAN et al. 1973). In vegetation ecology, the concept of computer assisted sampling was adopted by LAFRANCE (1972) in a pattern and ordination study of artificial communities. To my knowledge this is the only attempt to employ computer-generated, although not completely randomized samples in analyzing plot characteristics—ordination relationships.

For various purposes, SZŐCS (1979) developed a flexible computer program (CROCUS) offering a broad variety of sampling parameters. Randomly or systematically arranged plots of any size, orientation and three different shapes can be simulated, and distance-based sampling methods can be performed. Another program written by BONNICKSEN and STONE (1981) also contains plotless and plot sampling procedures including GREIG-SMITH's (1952) grid analysis.

As mentioned above, there are some fundamental problems associated with computerized sampling, which may introduce bias into the results. The first "defect" is due to the restriction that no overlap between sampling units and the boundary line of the mapped area is allowed. As a consequence, even though the plots are taken at random, the individuals close to the boundary will have a lower probability for being present in a random sampling unit than the others ("edge effect", O'REGAN and PALLEY 1965, WENSEL 1975). This is demonstrated by Figure 1a in which square units with orientation parallel to the edge are used for simplicity. Clearly, for any individual with distance from the boundary larger than or equal to the side length of plots, s, the probability of occurrence is proportional to s^2. If the distance is smaller than s, say x, the probability of being sampled is lower, because all random plots are deleted whose centroid would fall into the edge strip of width $s/2$. The reduced probability is proportional to $s \cdot x$, which is illustrated by the shaded part of each square drawn around the individuals as centroids (Fig. 1a). The result is that within the edge of width s the sampling intensity is continuously decreasing towards the edge. For this reason, if quadrat

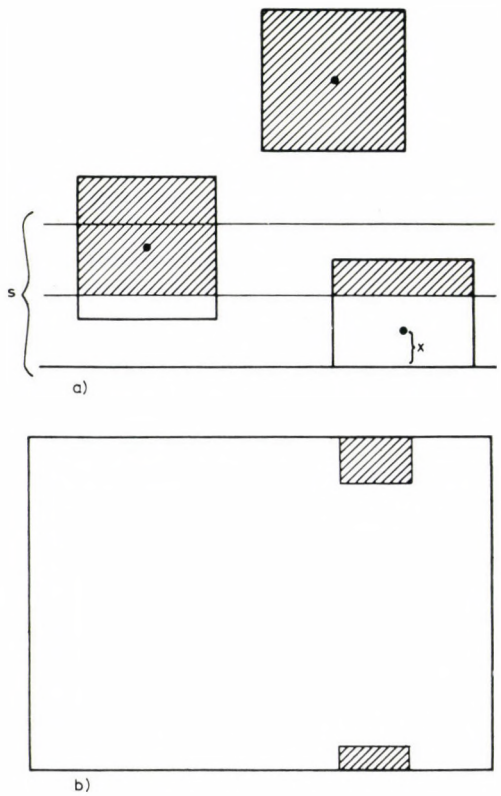

Fig. 1. Edge effect. a) Shaded areas are proportional to the probabilities for three individuals for being sampled. b) WENSEL's correction for edge effect

sampling is used in estimating, for instance, the volume of timber in a forest, the estimation will be biased. WENSEL (1975) described a technique to overcome this difficulty suggesting the inclusion of any incomplete sampling unit complemented by another fragment coming from the opposite side of the study area (Fig. 1b). Obviously, this strategy may help in estimating only some population parameters and species-individual diversity. If interest is centred upon interspecific associations, inter-plot resemblance coefficients, supraindividual diversity, etc., Wensel's technique is obviously inappropriate. It is felt, however, that in the latter cases the edge effect should not be corrected at all in a simulated study. This problem equally applies to field surveys, since random sample plots are never laid onto the boundary line of the study area. Theoretically, any field study is affected by edge effects although they become negligible as the study area increases. Thus, even though three maps used in this survey actually represent small parts of real communities, there is no reason for correcting an effect which is unavoidable in all studies. Of course, the scales of a field study and a simulated investigation are very different, but it seems immaterial concerning the recognition of principal spatial trends in vegetation analysis. The only, but very important consequence of the difference in scales is that the results from a computerized study (e.g., the size of characteristic areas) do not apply directly to the whole community from which the map was taken.

The second problem is related to the geometric representation of plant individuals on the maps. Whereas two-dimensional scattergrams may give a good approximation to the original pattern in forests, the description of grasslands and many other plant communities may be much less accurate this way. Centroids of plant patches and point clusters may well be used instead of the actual geometric shapes, but point representations are presumably not satisfactory for all purposes. However, the discrepancy between results based on point patterns and cover maps has yet to be examined. An objective of this study is to do this by comparing the results based on two different maps of the same area.

Another potential disadvantage is that random plots generated by the computer may be overlapping unless the strong restriction of taking only exclusive plots is forced on the sampling procedure (e.g., as in case of systematic sampling). If plot size or sample size increases, the area sampled with overlapping plots will also increase. Surely, this process results in increasing precision of estimates for population parameters and diversity indices [for the latter case evidence is found in NOSEK (1976)]. However, it is not yet known whether estimates of information theoretical characteristic functions (JUHÁSZ-NAGY and PODANI 1983) or expected resemblance (PODANI 1982, 1984) are biased as a result of such "oversampling". Therefore, the effect of overlapping among plots will also be analyzed in this study.

The majority of computerized sampling studies are concerned with the pattern of a single species (e.g., BONNICKSEN and STONE 1981), species-individual diversity (NOSEK 1976) and, in particular, with the performance of various sampling methods in estimating population parameters for a selected species (e.g., KULOW 1966, PALLEY and O'REGAN 1961). There is no doubt that digitized field data and simulated sampling may equally be useful in studying either small-scale community structure (WILLIAMS et al. 1969) or the influence of sampling upon the results of multivariate analyses (LAFRANCE 1972). Some other questions frequently raised in phytosociology, such as the determination of characteristic areas in plant communities or the estimation of inter-plot resemblance have not yet been investigated using the computerized sampling approach. In this study the main objective is therefore to examine how the information theoretical characteristic functions formulated by JUHÁSZ-NAGY and PODANI (1983) and expectations for four resemblance coefficients (SORENSEN index, RUSSEL–RAO index, simple matching coefficient, and Euclidean distance; see ORLÓCI 1978, and SNEATH and SOKAL 1973) are influenced by plant pattern and changes of sampling parameters. Of course, all possible aspects of this problem cannot be undertaken in a single survey, so atten-

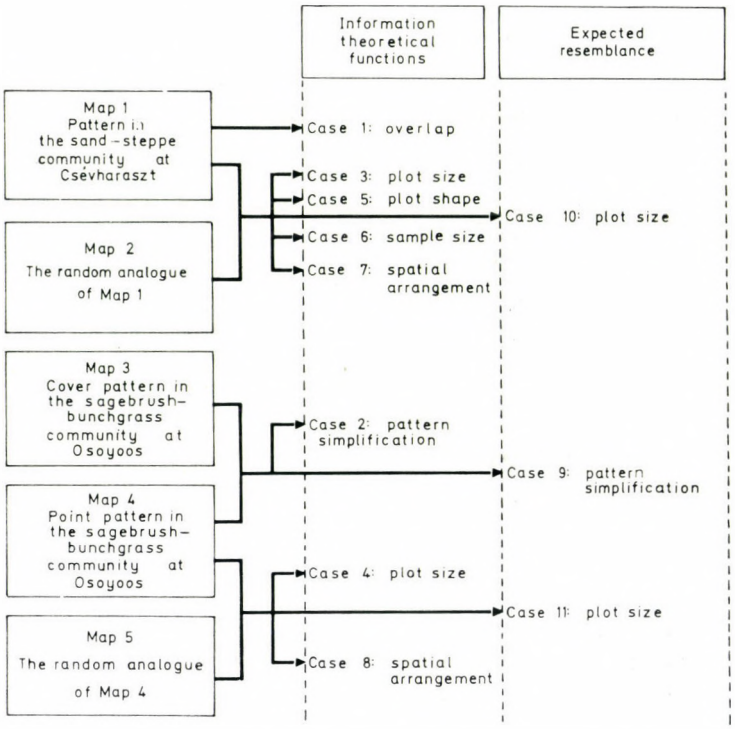

Fig. 2. Diagram illustrating the sampling experiments performed in the present study. The maps compared or analyzed, the functions calculated, and the conditions of sampling changed in each case are shown

tion will be paid only to relatively simple situations. The basic strategy is that real vegetation maps will be contrasted with simulated random patterns such that a particular sampling parameter is changed (primary process in the real space, cf. PODANI 1984). These changes are: increase of plot size or sample size, elongation of plot shape, and the transformation of systematic sampling design into a completely random arrangement of plots (sampling process). The different situations examined are summarized in Fig. 2, which demonstrates that interest will be focused on plot size changes in order to examine the potential usefulness of two different approaches to the characteristic area problem.

Material

Five maps were selected in such a way that homogeneous and heterogeneous communities, clumped and random distributional patterns are all represented to allow a comparative evaluation of results. One map was obtained from Z. SZŐCS, two others depicting different geometric images of the same plant assemblage were obtained by the author. In addition, two random (more precisely, pseudo-random) multi-species patterns were simulated with identical species numbers and abundances as in the real maps. These maps will be used as references to examine the departure of results from those based on the random distribution of plants.

Map 1 is the point pattern of the most abundant six species (Table 1) in a perennial sand-steppe at Csévharaszt (Kiskunság National Park, Hungary). The 2.4×10 m² area was mapped in 1973 by Z. Szőcs using his photocomputational technique (Szőcs 1977, 1979). Based on the photographs, the position of the centroid of each plant individual was digitized in form of two-dimensional Cartesian coordinates and committed to computer core. The digitized map was originally subjected to intensive pattern study by computerized sampling methods (Szőcs 1977). The area is fairly homogeneous and most of the species exhibit clumped spatial dispersion. The random analogue of this map is Map 2.

Map 3 was taken in a sagebrush-bunchgrass community in the Okanagan Valley at Osoyoos (British Columbia, Canada) in the summer of 1981 (Fig. 3). Due to the complexity of the vegetation, the photocomputational method was not used. Instead of this, an 8×20 grid—composed of 31.25×31.25 cm² cells, yielding a total area of 2.5×6.25 m²—was laid down to facilitate the mapping. The positions of plant individuals and patches were carefully recorded. A total of 23 species were found (Table 2). The actual spatial extension of the individuals of 15 species was regarded as point-like. For one species (*Artemisia tripartita*) both the position of stems and the perpendicular projection of living plant parts onto the ground were drawn. Other species (*Carex filifolia*, *Antennaria rosea*) and grasses (*Agropyron spicatum*, *Bromus tectorum*, *Festuca occidentalis*, *Koeleria cristata*, *Poa sandbergi* and *Stipa occidentalis*) were plotted as patches. Since this map cannot be readily used for computerized sampling, another map (Map 4, Fig. 4) was drawn to indicate only point patterns. In this map, the position of stems and the centroids of grass patches are shown or are represented by point-clumps. Map 4 is then a simplified, ready for digitization version of Map 3. However, the simplification reduces the information content of the map, and this fact has to be considered when evaluating the results. Despite its relatively small size, this area is not homogeneous, very few species occur throughout. The number of individuals on the left side of the map is

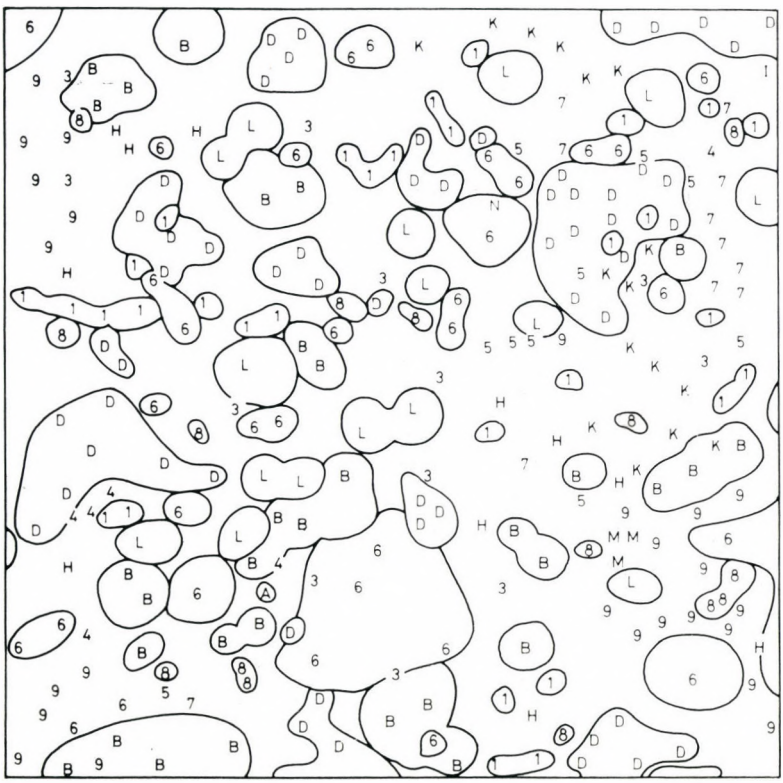

Fig. 3. Cover pattern in the sagebrush – bunchgrass community. Detail of Map 3 showing one-tenth of the total mapped area

Table 1

List of species occurring in Map 1. Nomenclature follows Soó *and* Jávorka *(1951)*

No.	Name	Number of individuals
1	*Koeleria glauca*	755
2	*Stipa pennata*	147
3	*Festuca vaginata*	287
4	*Polygonum aviculare*	48
5	*Tragus racemosus*	324
6	*Minuartia verna*	50
	Total:	1611

Table 2

List of species occurring in Maps 3–4. Nomenclature follows Scoggan *(1978)*

No.	Symbol on maps	Name	Number of individuals
1	1	*Poa sandbergii*	273
2	2	*Erigeron pumilus*	29
3	3	*Lupinus sericeus*	75
4	4	*Plantago patagonica*	492
5	5	*Collomia linearis*	148
6	6	*Artemisia tripartita*	259
7	7	*Madia exigua*	337
8	8	*Antennaria rosea*	205
9	9	*Achillea millefolium*	139
10	A	*Bromus tectorum*	126
11	B	*Agropyron spicatum* var. *inerme*	166
12	C	*Koeleria cristata*	27
13	D	*Carex filifolia*	426
14	E	*Phlox longifolia*	25
15	F	*Stipa occidentalis*	40
16	G	*Saxifraga integrifolia*	31
17	H	*Polygonum majus*	103
18	I	*Calochortus macrocarpus*	5
19	J	*Zigadenus venenosus*	1
20	K	*Erigeron corymbosus*	96
21	L	*Festuca occidentalis*	51
22	M	*Lithospermum ruderale*	22
23	N	*Castilleja pallescens*	1
		Total:	3077

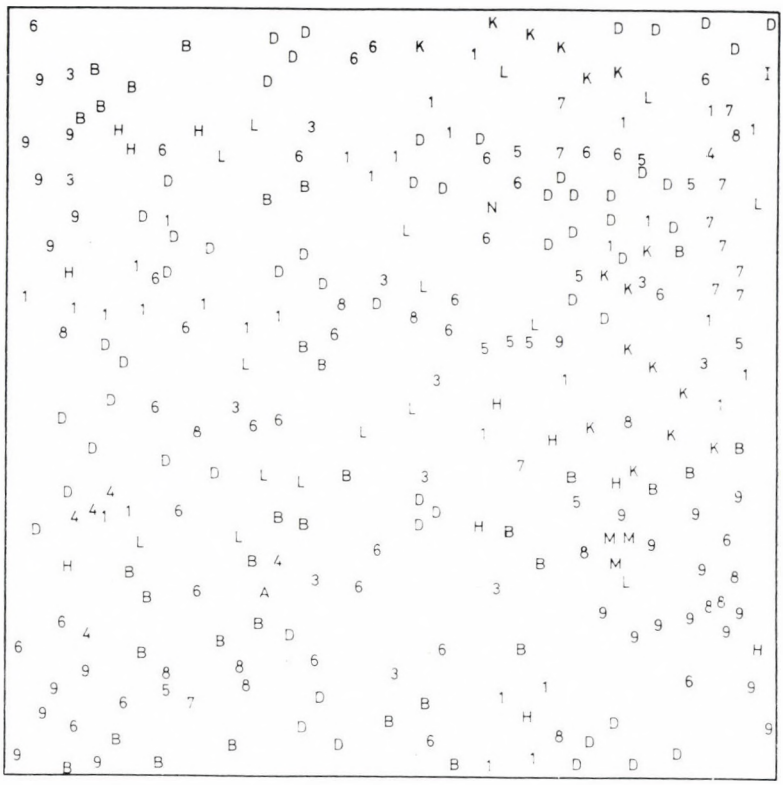

Fig. 4. Point pattern in the sagebrush – bunchgrass community. Detail of Map 4 corresponding to the one shown in Fig. 3

much higher than on the other side, due to the abundant presence of *Plantago patagonica*. Some species are almost completely restricted to the middle or the right part of the area. The random analogue of Map 4 is Map 5.

Methods

Since the existing computer programs lack some options required by the present study, it appeared practical to develop my own sampling simulator program package. Three FORTRAN programs applicable to point patterns have been written.

Program ELSAM is designed to simulate random plots of circular, rectangular or elliptical shape with random or uniform orientation. The map and the sampling units may be drawn using a HP-7221A plotter. The standard output is a species-by-sampling units matrix of counts written onto disk. Since the plots are independently selected, the possibility of their overlap is not excluded.

The sampling process (PODANI 1982, 1984) which includes systematic, restricted random and fully random sampling may be carried out by program SAMPROC. Plotting subroutine is not provided, only circular and rectangular plots and square blocks can be specified. If required, only systematic sampling is performed and in this case the output consists of a single matrix. Otherwise several matrices will result, each corresponding to one particular stage of the process.

Random pairs of plots are simulated by program EXPRES which in turn calculates the expectation of resemblance coefficients. In this program it is ensured that the paired plots are non-overlapping.

Florula diversity and related information theory functions were calculated by program INPRO described first in JUHÁSZ-NAGY and PODANI (1983). The input of this program is a species-by-quadrats matrix. The result includes the actual values for characteristic functions and the number of manifested species combinations. If required, the frequency distribution of combinations is also printed.

On Map 3 the sample plots were manually placed using a table of random numbers. In this case expected resemblance was calculated such that random pairs of plots were selected from the data matrix. In order to ensure independence among these pairs, every plot was considered once. Expectations for four binary coefficients (SORENSEN index, RUSSELL–RAO index, simple matching coefficient, and Euclidean distance) were calculated for all types of maps.

Results

Information theoretical functions vs sampling characteristics

Case 1: The effect of overlap among plots

This problem was examined using the Csévharaszt map (Map 1). Program ELSAM generated 250 random and potentially overlapping plots at each of the ten plot sizes previously selected. The plot shape was square, the sizes ranged from $10 \cdot 10$ cm^2 to $60 \cdot 60$ cm^2. Non-overlapping plots with similar sizes were placed in systematic arrangement by program SAMPROC. The sample size was 64 with the largest plots forming a continuous grid. The relationships of characteristic functions and plot size are given in the diagrams in Fig. 5. It is seen that the two results are in very close agreement, the corresponding curves are similar in shape. Local distinctiveness and florula diversity are high within the interval [0.1, 0.2] in both cases. The actual maxima occurred at $40 \cdot 40$ cm^2 when the sampling was systematic, at $37.5 \cdot 37.5$ cm^2 when the plots were randomly arranged. Nevertheless, the peaks are not striking and the differences in maximum areas indicated appear negligible. Further correspondence between the two results is that associatum shows less obvious trend than the other two functions. A relatively high level is maintained within a broad range of plot sizes and no significant peaks can be seen. These observations suggest that overlapping plots produce no artifacts and can be used to estimate information theoretical and probably many other characteristic functions.

Case 2: The effect of pattern simplification

The discrepancy between results based on two geometric images of the same area was examined using the Osoyoos maps (Maps 3–4). The plot shape was circular, with radii ranging from 0 cm to 75 cm. The sample size was 250 both in the simulated and the manual sampling. Figure 6a shows the change of the number of species combinations, Figure 6b illustrates the characteristic functions. Surprisingly, the results are more similar than expected. The position of peaks is invariant, the maximum of local distinctiveness and associatum occurs at radius of 25 cm in both maps. Florula diversity does not exhibit a peaked effect, there is a characteristic interval between 15 and 25 cm, rather than a particular well-indicated area. Similarly, the number of species combinations (NSC) is very high at several plot sizes if the cover map is used. For the point pattern, however, NSC has a well-defined maximum. Another striking difference between the results is that the actual values of characteristic functions at

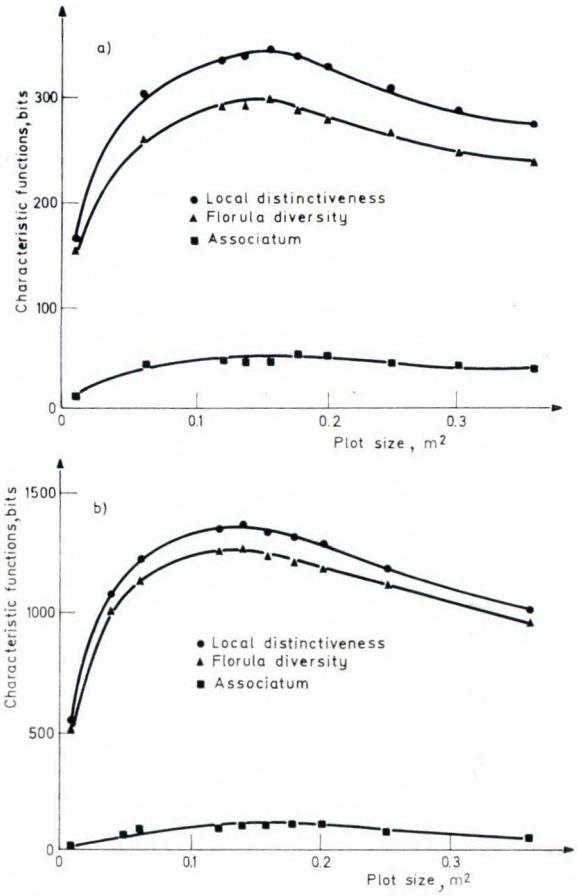

Fig. 5. Case 1: The effect of the size and arrangement of plots on characteristic functions in the sand-steppe community at Csévharaszt. a) Systematic sampling (no overlap allowed). b) Random sampling (plots may overlap). Note that differences in magnitude are due to differences in sample size

small plot sizes tend to be higher in case of the cover map. These are the only consequences of the divergence between the two contrasting pattern representations of the same area. The congruence of results is unexpected and probably due to the fact that 15 of the 23 species are represented by points in both maps. This number is large enough to ensure invariability in the size of characteristic areas. Of course, this is not to say that the present findings have unrestricted validity, since the distortion introduced by simplification to point patterns depends on the number of species and their individuals with patchy spatial appearance. Nevertheless, in case of the Osoyoos map simulated sampling may well be used instead of the more laborious manual sampling.

Cases 3–4: The determination of characteristic areas

The range of plot sizes by which the Csévharaszt map was sampled in Case 1 was fairly narrow to facilitate a satisfactorily large sample size in systematic sampling. Therefore, the map was re-sampled by a series of circular plots with radii ranging from 5 to 75 cm. The

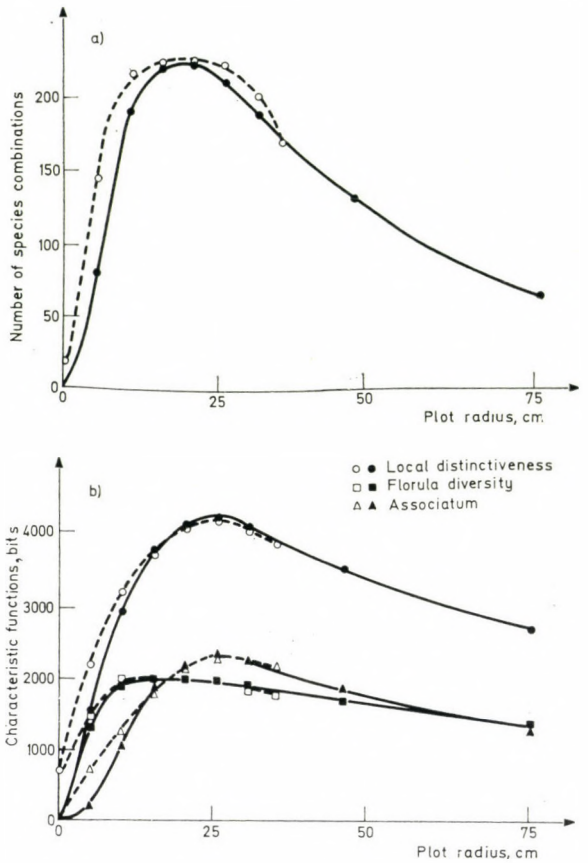

Fig. 6. Case 2: The effect of plot size and pattern simplification on the number of species combinations (a) and characteristic functions (b) in the sagebrush – bunchgrass community. Dotted line and open symbols: manual sampling of the cover map, solid line and full symbols: simulated sampling

sample size (250) was not changed. Preliminary results suggested that the critical range of characteristic areas was between circles with radii 15 and 25 cm. To test whether the peaks occurred consistently at the same point, three replicate samples were taken at plot radii 15, 20 and 25 cm. The random point pattern corresponding to the Csévharaszt map was also sampled with similar plot and sample sizes. The results are shown in Figs 7–8.

Figure 9 illustrates the results for the actual Osoyoos map and the corresponding randomly generated pattern. In these cases sample size was 300, plot radius ranged from 5 to 75 cm.

Figures 7–9 demonstrate that local distinctiveness, florula diversity, associatum and NSC first rapidly increase and later slowly decrease with increasing plot size, regardless the type of the spatial distribution of species. This observation supports the findings by JUHÁSZ-NAGY (1967, 1976) and JUHÁSZ-NAGY and PODANI (1982) who made similar surveys using field data.

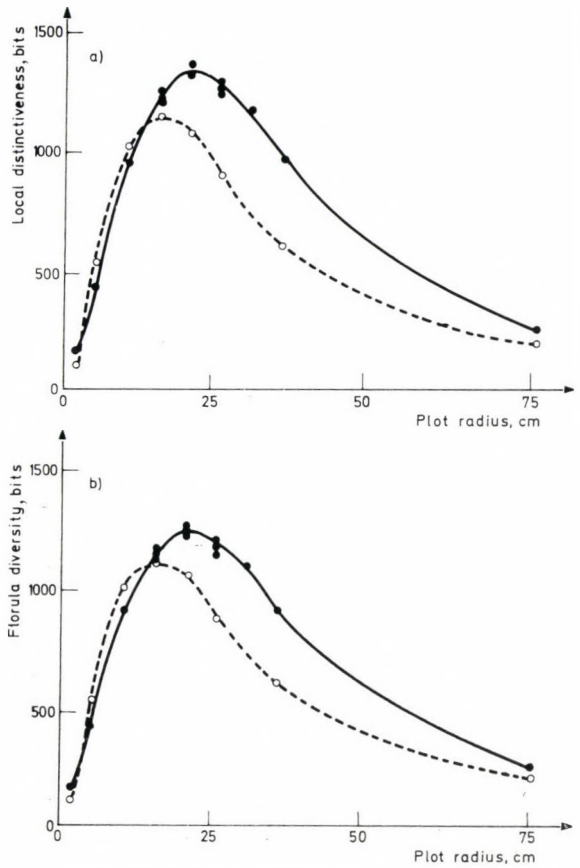

Fig. 7. Case 3: Dependence of local distinctiveness (a) and florula diversity (b) on plot size and spatial pattern in the sand-steppe community. Dotted line and open symbols: random pattern, solid line and full symbols: real map. Curves fitted by eye

The replicate samples from the Csévharaszt map indicate that there is a unique maximum for local distinctiveness and florula diversity at plot radius of 25 cm, whereas the maximum of NSC occurs at 20 cm. For the randomly dispersed population the corresponding areas are smaller. In practice, at small plot sizes there is no substantial difference between the random and the actual population. However, at about the size of characteristic areas the diversity of the actual vegetation is much higher than that of the random community, and the deviation from randomness apparently increases as the plots are further enlarged. Later the difference tends to disappear suggesting that in a homogeneous vegetation there is a fairly large plot size at which the type of spatial distribution of species becomes immaterial.

The change of associatum versus plot size (Fig. 8a) is less obvious. Although both curves have double peaks, this is not sufficient evidence for bimodality. One could easily select points from the replicate triplets such that the maximum occurs at either of 15, 20 or 25 cm plot radius. Therefore, Fig. 8a rather suggests that the estimation of associatum is more influenced by random fluctuations than are the other functions. Perhaps there is no

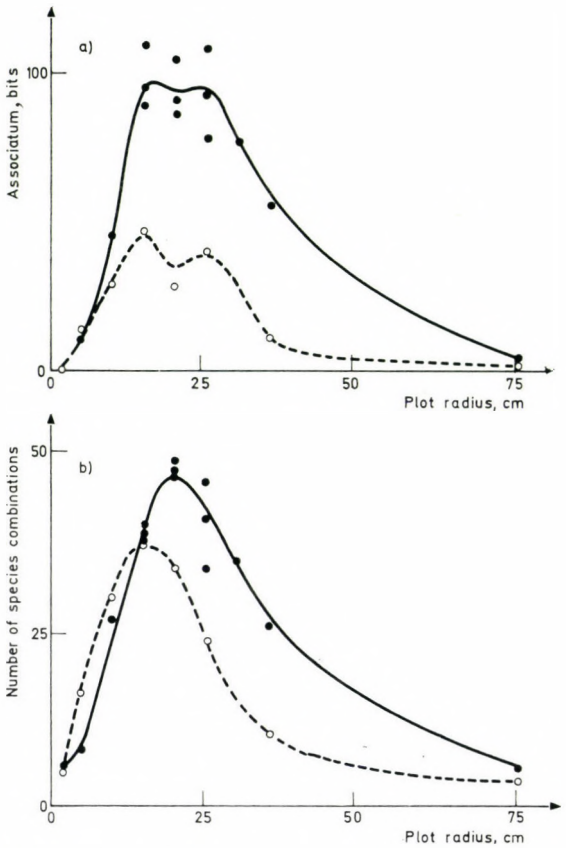

Fig. 8. Case 3: Dependence of associatum (a) and the number of species combinations (b) on plot size and spatial pattern in the sand-steppe community. Dotted line and open symbols: random pattern; solid line and full symbols: real map. Curves fitted by eye

particular maximum area but a relatively wide range of plot sizes (characteristic interval) with consistently high associatum values. The other Csévharaszt results (Case 1, see Fig. 5) also support this observation.

The Osoyoos results (Fig. 9) are similar to the Csévharaszt ones in many respects. Local distinctiveness and NSC both have a clear maximum at 25 cm, and the characteristic areas are consistently smaller in the random "community". However, the decrease of characteristic functions beyond the maxima is very slow, and the deviation from the random situation rapidly increases with plot size, at least within the range of plot sizes used. Contrary to the Csévharaszt results, the curve of associatum has a distinct peak and it is the florula diversity for which no well-defined maximum area was found. In the random population the number of species combinations reaches a higher maximum than in case of the actual community.

It may be concluded that differences in the above findings are indicating differences between the structure of the communities being analyzed. The post-maximum slope of characteristic curves and their deviation from the random case are good indicators of homogeneity (or heterogeneity). Well-defined maxima may be expected for local distinctiveness and NSC

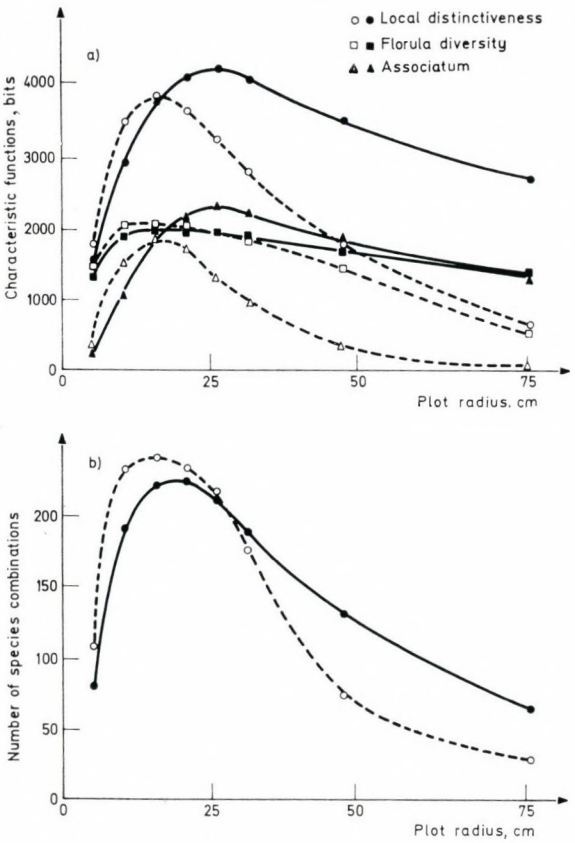

Fig. 9. Case 4: Dependence of characteristic functions (a) and the number of species combinations (b) on plot size and spatial pattern in the sagebrush – bunchgrass community. Dotted line and open symbols: random pattern; solid line and full symbols: real map

regardless the type of species pattern. Florula diversity, however, is more influenced by spatial factors and the maximum is closely approximated at various plot sizes in heterogeneous or species rich communities. The results also indicate that associatum is likely to be influenced by random fluctuations if the number of species is low. Increase in species number diminishes this effect, as the Osoyoos results clearly demonstrate.

Case 5: The effect of plot shape

The change of characteristic functions over plot size in the sand-steppe community was examined using two different isodiametric shapes: square (Fig. 5) and circular (Figs 7–8). The maxima for local distinctiveness and florula diversity occurred at 37.5 · 37.5 cm^2 (0.1406 m^2) and at plot radius 20 cm, which corresponds to an area of 0.1256 m^2. The difference between these two maxima seems negligible, because the area increments for the circular plots were much larger than those for square units.

The spatial process representing the elongation of plots with a constant area was examined using the Csévharaszt map. The plot size selected was 0.122 m^2, with the following

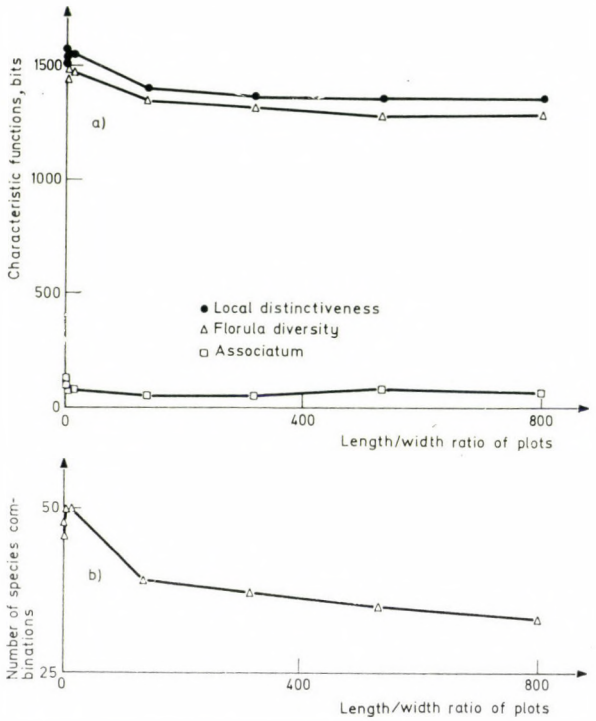

Fig. 10. Case 5: The influence of plot shape on characteristic functions (a) and the number of species combinations (b) in the sand-steppe community

series of length/width ratios: 1 : 1, 2 : 1, 3 : 1, 5 : 1, 12 : 1, 135 : 1, 325 : 1, 543 : 1, 818 : 1. The last terms of this sequence represent extremely long shapes which give a close approximation to the linear plots. As GREIG-SMITH (1964) pointed out in such a series the side length of plots increases as the ratio increases, introducing uncontrolled edge effects into the results. The only situation in which this problem could be ignored is if all the plant individuals were point-like, but this condition is never satisfied in natural vegetation.

The effect of the elongation of sampling units on the characteristic functions is demonstrated by Fig. 10. It is seen that plots with low length/width ratio result in a more diverse sample than the long units, even if fairly homogeneous point patterns are examined. Although no other experiments were made, it seems obvious that this effect is more emphatic in a heterogeneous vegetation, since longer plots are more likely to include species that are spatially isolated. However, differences between shapes that are commonly used in the phytosociological practice (square and short rectangles) do not appear significant.

Case 6: The effect of sample size

Since absolute values of characteristic functions are directly proportional to the sample size, standardization is required. Local distinctiveness is normalized if divided by its possible maximum. Florula evenness (JUHÁSZ-NAGY and PODANI 1983) may be used instead of florula diversity. The knowledge of these standardized measures is sufficient to predict the behavior of normalized associatum, which would be very difficult to calculate directly. NSC requires no standardization.

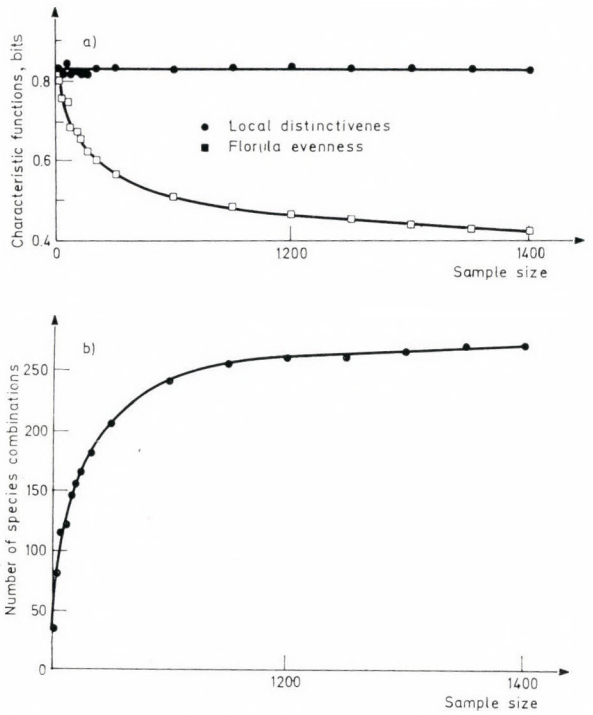

Fig. 11. Case 6: The effect of sample size on characteristic functions (a) and the number of species combinations (b) in the sand-steppe community

Figure 11 indicates that in case of local distinctiveness, sample size is a matter of statistical estimation. A small number of plots is obviously inappropriate to yield reliable estimates, but beyond a critical number, the results are not fluctuating significantly. Florula evenness, however, decreases monotonically, and therefore the normalized associatum increases as the number of plots increases. Its principal reason is that the maximum number of species combinations, which may be potentially manifested in the sample at the given plot size, is not approached even by more than two thousand plots (Fig. 11b). As a consequence, florula evenness estimates coming from different surveys can be compared only if the sample sizes are equal. It is noted that in species/individual diversity studies a similar relationship was found between evenness and sample size by other authors (see PIELOU 1975).

Cases 7–8: The effect of the spatial arrangement of plots

The Osoyoos and Csévharaszt maps were subjected to the sampling process which involved systematic, stratified random and random sampling with many intermediate stages. The sample size was considerably large, 250 and 262, respectively. Two plot sizes (20 · 20 and 5 · 5 cm^2) were used in both cases. The results are summarized in Fig. 12.

It is seen that the use of small compartments gives deviating estimates for the characteristic functions. As the design approaches full randomization, this fluctuation tends to disappear, and the last two stages of the process yield almost identical results. In case of the Csévharaszt community, systematic sampling gave the highest estimates for local distinctiveness and florula diversity, but no similar tendency is observed for the Osoyoos data. The

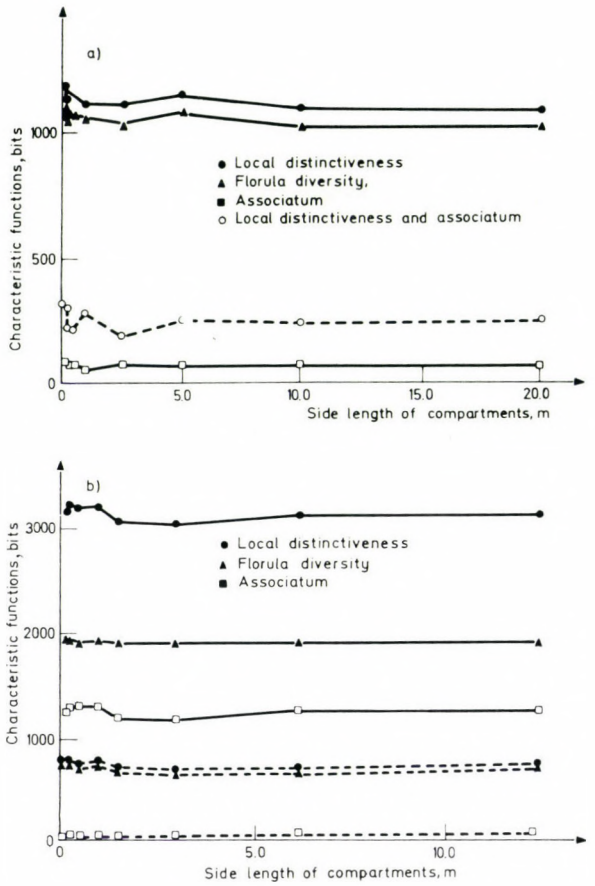

Fig. 12. Case 7: The effect of the spatial arrangement of plots on characteristic functions in the sand-steppe community (a). Case 8: The same effect in the sagebrush – bunchgrass community (b). Solid line: 20×20 cm^2 plots, dotted line: 5×5 cm^2 plots

results support the view that there is a direct relationship between the arrangement of sample plots and the precision of estimates. Systematic and stratified random sampling is not suggested for use when the goal of the survey is statistical estimation. The starting position of the grid and the size of compartments are strong influential factors. For these reasons, randomized sampling appears a more straightforward design in estimating these characteristic functions.

Expected resemblance vs plot size

Case 9: The effect of pattern simplification

It was shown in Case 2 that the simplification of Osoyoos map into a point pattern induced no significant changes in the information theoretical characteristic functions. According to Fig. 13, the expectations for simple matching coefficient and binary distance are also

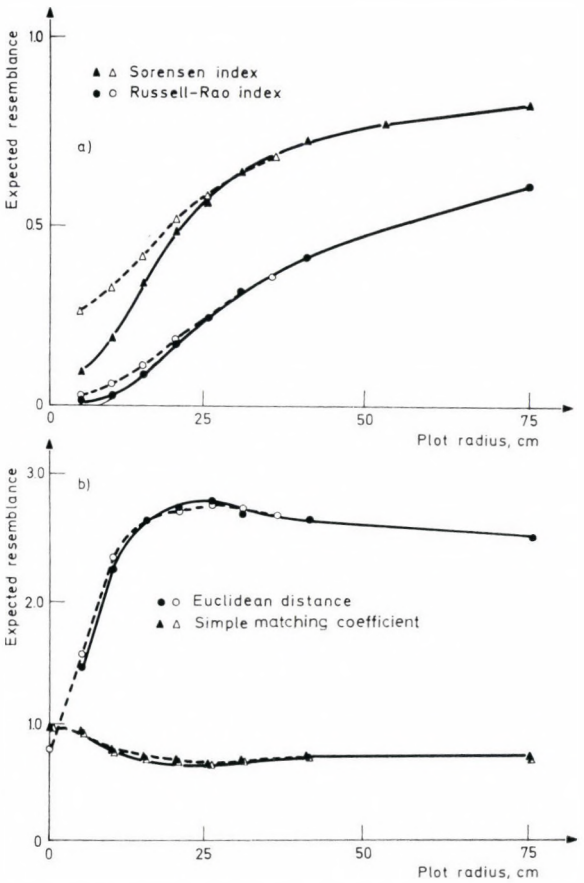

Fig. 13. Case 9: The effect of plot size and pattern simplification on expected resemblance in the sagebrush – bunchgrass community. Dotted line and open symbols: manual sampling of the cover map; solid line and full symbols: simulated sampling

little affected. The only considerable distortion occurs in case of coefficients that do not take "negative" matches into consideration (SORENSEN index and RUSSEL–RAO coefficient). However, the deviation between the corresponding curves decreases as plot size is increased. At about the area of maximum local distinctiveness the results are almost identical. The conclusion is that computerized sampling of point patterns leads to underestimation of the true expectation for these indices at small plot sizes. This fact should be considered in evaluating the results.

Cases 10–11: Expected resemblance and characteristic areas

From a pragmatic point of view it may be an important question whether expected resemblance is applicable to determine characteristic areas of plant communities. In terms of expected resemblance, a theoretical maximum area is defined as a plot size at which the expectation for inter-plot distance (or dissimilarity) is maximum, so that the sample hetero-

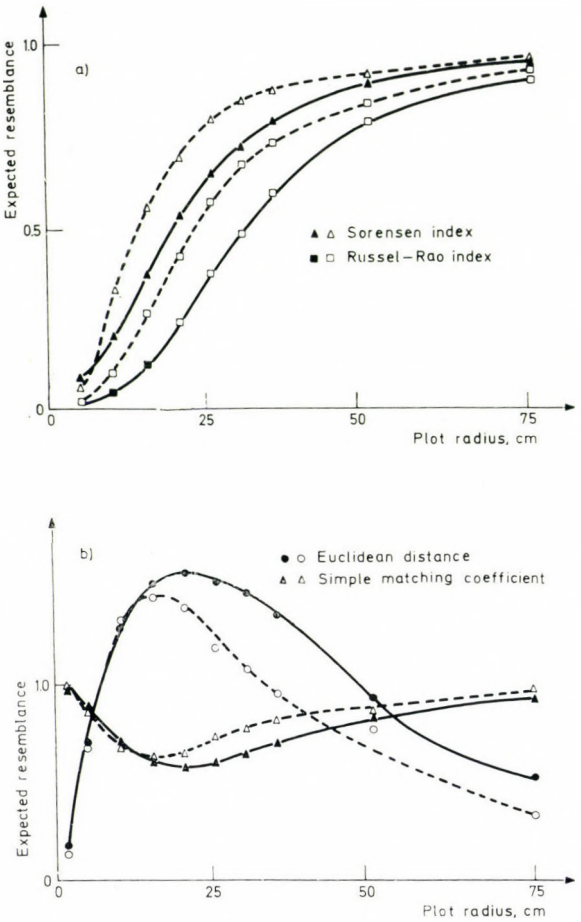

Fig. 14. Case 10: Dependence of expected resemblance on plot size and spatial pattern in the sand-steppe community. Dotted line and open symbols: random pattern, solid line and full symbols: real map

geneity is also maximum. By definition, at minimum area the distance becomes zero. It is easy to see that in the binary case, as in this study, this minimum area equals the one defined in terms of florula diversity (i.e., distance may be zero only if all sample plots are similar in floristic composition). The maximum areas determined using the two approaches may be different, however, since maximum florula diversity does not necessarily imply maximum expected distance.

As already seen in Case 9, and also in Figs 14a and 15a, two binary coefficients (SORENSEN index and RUSSELL–RAO coefficient) monotonically increase over plot size. This is in fact a consequence of the exclusion of "negative" matches. Thus, only minimum area can be unequivocally determined, i.e., the plot size at which expected similarity is unity. It would be difficult, on the other hand, to recognize a point or even an interval which would correspond to the most diverse sample. The determination of maximum area by measuring the slope of

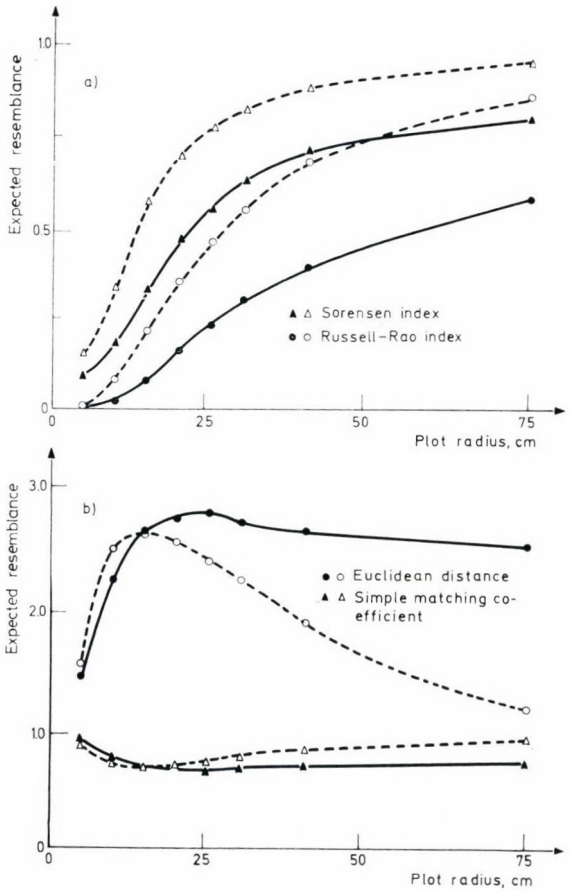

Fig. 15. Case 11: Dependence of expected resemblance on plot size and spatial pattern in the sagebrush – bunchgrass community. Dotted line and open symbols: random pattern; solid line and full symbols: real map

the curve seems rather arbitrary. As with the species/area curves, the selection of a point where the curve becomes flattened would be even more an arbitrary step.

The concept of distance-related resemblance appears more meaningful in seeking maximum areas. For Euclidean distance and simple matching coefficient, which can be calculated from one another, extreme values are indicated both in the real and the random maps (Figs 14b and 15b). Furthermore, there is a good agreement between the results obtained by these measures and the information theory functions. In the sagebrush community and its random version, the two different approaches indicate the same maximum areas. In the Csévharaszt community the area of maximum expected distance equals the plot size where maximum NSC was found. It seems then that the distance-based approach may replace the other without much loss of information. The significance of this finding lies in the fact that the estimation of florula diversity usually requires very large sample size.

The effect of spatial pattern on the resemblance of plots is also demonstrated by Figs 14–15. As expected, the sample plots from random communities are more similar to one another

than those from the real maps, unless the plots are too small. In a homogeneous community, the deviation from randomness is not significant and tends to decrease at large plot sizes (Fig. 14). In the heterogeneous community of Osoyoos, this trend cannot be observed within the range of plot sizes used (Fig. 15). Other difference is that the peak at 25 cm is not distinct and the decrease in expected distance is very slow. This is yet another indication of heterogeneity.

Concluding remarks

The findings of the present study suggest that simulated sampling is in many cases an efficient substitute for the more laborious field sampling. The analysis of vegetation maps by means of computer programs is useful when the relationships between characteristic functions and plant pattern are investigated under different conditions of sampling.

It was found that the random arrangement of potentially overlapping plots is not inferior to systematic sampling. Moreover, it is expected to give more reliable estimates for the characteristic functions since there is no upper limit of sample size. The edge effect is considered an unavoidable concomitant of plot sampling and its correction is not recommended when characteristic areas are to be determined. The sizes of characteristic areas (namely the maximum area in terms of information theory functions and expected resemblance) were little affected by the simplification of an actual vegetation map, showing horizontal projection of several species, into a point pattern. Estimates for characteristic functions and expected resemblance based on the contrasted pattern representations differed significantly only at very small plot sizes that are not used in practice anyway. One is warned, however, that simplification of plant pattern cannot always be done without much loss of information, the success is case-dependent.

The experiments with characteristic functions justified the results deriving from earlier field studies. Florula diversity, associatum, local distinctiveness and the number of species combinations in the sample are dependent on plot size and the spatial pattern of species. In a homogeneous vegetation, these functions have maxima at a certain plot size or within an interval of sizes, indicating characteristic areas at which the community is found in its most diverse development. If the sampled area is heterogeneous, characteristic areas or intervals may also be indicated as the Osoyoos results demonstrate. In theory, these functions may be best used to determine optimum plot size in presence/absence-based multivariate studies. However, the practical usefulness of this approach is limited since the estimation of florula diversity requires an unrealistically large sample size unless the number of species is very low. The problem is further complicated by the fact that the characteristic areas may vary with community types.

One alternative to the information theory functions is expected resemblance which can be derived from relatively small samples. The results obtained

by computer simulated sampling showed that distance-related binary coefficients are meaningful in seeking characteristic areas. There was a good agreement with the information theory approach although in the heterogeneous case the indication of maximum area was less obvious. This observation suggests that florula diversity is closely related to distance, whereas the relationship between similarity coefficients ignoring "negative" matches and diversity is unclear.

Characteristic areas are found in randomly simulated communities analyzed using both approaches. Thus, the existence of characteristic areas is a mathematical necessity, and the actual sizes are determined by the number of "species" and "individuals" per unit area (density) in the simulated community. In addition to species number and abundance, characteristic areas of real communities are of course also influenced by plant pattern, and the departure from the random situation offers a possibility for evaluating community structure. In the examples analyzed the influence of plant pattern was clearly demonstrated: the maximum areas for expected distance, florula diversity and related functions were always larger in the real maps than in the random analogues. Further simulation experiments are necessary to reveal the relative importance of species number, abundance and pattern in determining the characteristic areas of a community.

Parameters of sampling other than plot size were also studied. Plot shape appeared a less influential factor than size. The change of characteristic functions was little affected at the beginning of the elongation process suggesting that the choice between square and shortly rectangular quadrats is not crucial. In theory, however, isodiametric plots should be preferred for typification since this shape is the less sensitive to vegetational heterogeneities. Very long plots cannot be recommended in general, but in special cases (when the plants are point-like and the objective is estimation of population parameters for a single species) they can prove more efficient than the others.

The increase of sample size is usually the best way to increase the precision of estimates. The only exceptions are some specific derived variables normalized by theoretical maxima that cannot be observed at small sampled areas (small plot or sample sizes). Florula evenness is an example, which is expected to decrease until all species combinations potentially manifested in the sample are captured by sampling. Since this number is usually very large, the change of florula evenness over sample size is of no practical value. Results derived from different surveys can be compared only if the sample sizes were equal.

Experiments with the sampling process demonstrated that the precision of estimates is influenced by the spatial arrangement of plots. Systematic designs may result in unreliable estimates, but the fluctuations tend to disappear as the sampling approaches full randomization.

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DEGRADATION STAGES IN A XEROSERIES: COMPOSITION, SIMILARITY, GROUPING, COORDINATION

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The paper deals with a secondary xeroseries, i.e. degradation stages brought about under the influence of grazing in a hill-country. Some dominant species have a decisive role in bringing about these stages and are of importance for their identification. The results suggest that at a low degree of degradation the cover values of species differ with vegetation types (stages): the change of cover in the degradation process is a general coenological phenomenon and is more important than other, qualitative aspects (e.g. preferential phenomena such as the separation of diagnostic species). The multivariate methods applied (agglomerative and divisive clustering methods and PCA ordination) proved to be efficient in describing the closely related stages. The distinction between the groups is clear. Homogeneous group formation—according to the dendrograms—was shown in types with a moderate extent of perturbation. The fusion levels of groups occur at irregular intervals suggesting that the degradation of the grassland does not take place in even steps either. The extent of coordination measured by the average similarity and the CV values of samples within the vegetation types is the lowest in the first and last stages of the degradation process.

Introduction

Coenodynamical problems receive more emphasis in recent phytosociological surveys. The overwhelming majority of studies have risen from a difficult situation in which the sociologist had not the opportunity to set up a systematic long-time experiment on vegetation dynamics, while there existed a usually varied topographic situation with more or less regularly spaced vegetation types, and the transformation of spatial pocesses to temporal ones was mostly one of the key tasks.

The knowledge of evolutionary relationships among vegetational units is often of basic importance. Sometimes, in cases when the spatial-temporal correspondence is simple as with a succession on an inundation area the relationships are obvious, while in other cases it is less so. The task is particularly difficult when certain phases of processes taking place in shorter periods of time are analyzed, rather than successional changes covering in a long period. Most degradation processes are of this type. Let us think, for example, of various grasslands where under the influence of a regular or periodical grazing of varying intensity and of other external effects succession processes differing in tendency and intensity may start and take place at the same time, producing different stages of degradation and regeneration.

The paper deals with the internal dynamics of a grazed slope steppe meadow. The dynamics is induced by anthropogenic-zoogenic affects so that the area is not evenly influenced but, as it will be seen, at an intensity continuously decreasing along a gradient. Thus, the experimental basic situation which also motivates the questions raised, is: the discrete states of vegetation as opposed to the continuous character of the effects.

A group of questions given below can be regarded as general in the sense that they might also be asked in the case of other objects. These are:

How do the stages separate from one another (what is the extent of distinction)?

How frequently are the stages repeated in space (what is the degree of "self-reproduction")?

Considering its stages is degradation an even process?

Furthermore: Are the classification and ordination methods recently used suitable to answering the above questions and describing degradation?

The group of special questions includes:

What is the origin of the rich species composition?

How has the present state of vegetation come into existence? How is it modified by grazing?

What is the phytosociological value of the vegetation types observed?

Vegetation types*

Spatial distribution

Clearly visible stratified degradation series develop at the feet of the Northern Hungarian Mountain Range (of medium height). On hilly areas bordering the contiguous forests and contiguous arables animal farming and grazing shape the vegetation following deforestation. The study area is a dry hill-country at the southern foot of the Bükk Mountains, a part of the range, at the village of Tard (north of the town of Mezőkövesd). The study area chosen is situated on a broken relief, at a height of about 200 m above sea level. For the details, the characterization of the geological and soil conditions and the description of the vegetation see VIRÁGH (1982).

The reconstructed preliminaries: a pre-deforestation state. The gentle hilly country surrounding the study area becomes lower and lower southwards until merging with the Great Hungarian Plain. The first steeper hills appear at the village of Tard. It is a marginal area from the point of view of vegetation geography, too. On the study area the climatic zonal forest preceding the deforestation was *Aceri tatarico-Quercetum* reaching this far from the Great Plain, as proved by relic species (*Quercus pubescens*, *Acer tataricum*, *Nepeta pannonica*, *Phlomis tuberosa* etc.) and remnant forest fragments (tree groups). The steep northern slopes may have been covered by some closed forest association of extrazonal appearance as suggested by the nearness of closed oak forest (the *Quercetum petraeae-cerris* forest zone).

The initial stage following the deforestation is represented by a *Calamagrostis epigeios* grassland and a *Danthonia alpina* dominated meadow. *Calamagrostis* has survived in small valleys, or in some cases in the upper quarter of the slope as small stands close to the forest remnants (shrubs). A forest steppe meadow rich in *Festuca rupicola* covers only smaller areas. A related steppe meadow with a great richness of species (*Pulsatillo-Festucetum rupicolae*) is also found today only in small patches. Under the influence of perturbing factors some high-stalked or agressive propagating monocots become dominant. These are capable of forming a composition of their own, preventing the intrusion of other species or making the surroundings unfavourable for them. In any case it was obvious that in separating and denominating the different vegetation types we were directed by the outstanding, physiognomically conspicuous dominant and abundant species.

* Vegetation type is understood here as the smallest visible unit of the vegetation, irrespective both of the phytosociological value (i.e. its place in the hierarchy of communities suggested by the Zürich–Montpellier school) and permanency in time. In this paper this term is equally used for the stabilized subclimax communities and different developmental stages.

On the upper stretches of slopes and on ridges grasslands with *Agropyron* repens as dominant species developed, while on more exposed slopes *Chrysopogon gryllus* dominated larger stands occur. In a mid-slope to slope-foot situation *Bothriochloa ischaemum* dominated swards, while at the foot of slope a selectively grazed vegetation type with dwarf grasses and *Leontodon hispidus* as dominant species are found.

On the steeper northern slopes the former forests of submountain character have been replaced by a xeromesophilous meadow-like grassland (*Cynosureto-Festucetum rubrae agrostidetosum tenuis*).* Its species composition unambiguously indicates the submountain origin. It can be considered a subclimax just like *Pulsatillo-Festucetum rupicolae.*

The present picture of the vegetation is thus characterized by a high patchiness which, being an inherent feature of the vegetation anyway, is greatly affected by the topographic conditions, erosion, and increased by treading and grazing. Accordingly, extremely dry spots alternate with patches of somewhat better water regime, soils rich in nutrient and shallow, overtrampled and overgrazed areas. The effect of grazing can be clearly seen in a unidirectional section. The extent of degradation increases towards the bottom of the slope, a place more frequented by the animals if only for topographic reasons (smaller angle of slope). The hilltop is better protected in spite of its mild slope because the animals are driven away from the surrounding fields.

References to the literature:

Calamagrostis epigeios stands develop in the forest steppe, oakwood, beechwood or even in the spruce zone, that is, their phytosociological range is very wide. Soó (1964) thinks it to belong to the *Chamaenaerion angustifolii* alliance (*Senecioni-Chamaenaerietum calamagrostetosum epigeiotis*), nevertheless its independence as association in terms of diagnostic species has not been proved.

Pulsatillo-Festucetum rupicolae: description in Virágh 1982, Máthé and Kovács 1962.

Cynosuro-Festucetum rubrae agrostidetum tenuis: characterized by Máthé and Kovács (1961–62). On our study area it is a case of extreme stands advanced towards the Plain.

Danthonia-Festuca secondary grassland is known to develop in other places of the hilly margins of the Northern Hungarian Middle Range, too; its coenological description has to be waited for.

An exact description of *Agropyron* and *Chrysopogon* dominated grasslands is also lacking. It should be noted that tabulated material that could be really well used is hardly available (unlike the nomina nuda).

The distribution of vegetation types in space is shown in Fig. 1. The reason for constructing the figure partly was to get the clue to the relations of the vegetation types on the basis of their spatial contacts. The map is naturally suitable also for the representation of the relative extension of each vegetational type, further for the documentation of the influence of angle of slope and exposure. It is seen, for example, that the primary (natural, semi-natural) types are isolated, the stands being surrounded by secondary types.

Each vegetation type was sampled using 5 replicate plots of 2×2 m size. Floristic data and cover estimates were recorded. For the localization and identification of the quadrats see Fig. 1.

A hypothetical successional scheme

The spatial arrangement of vegetation types in the study area suggests the existence of a mostly secondarily produced coenocline. The two extremes are represented by the forest steppe meadow and the *Leontodon* type. Since the beginning of the series is formed by a more

* See on the vegetation map (Fig. 1.) the areas without marking.

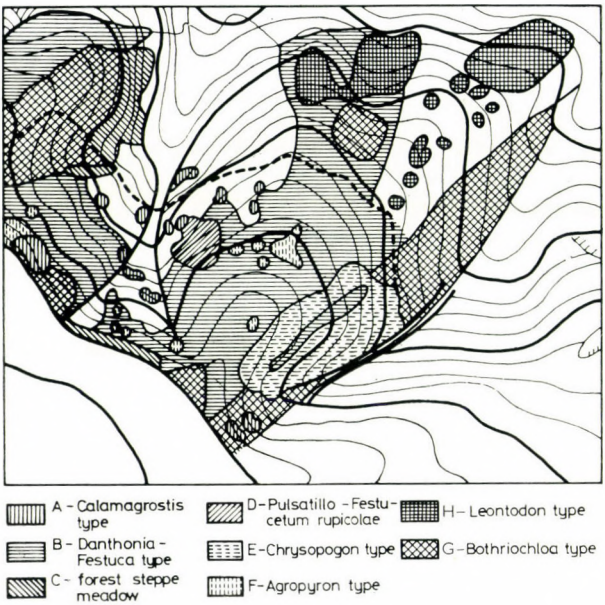

Fig. 1. Vegetation map (1 : 4 000)

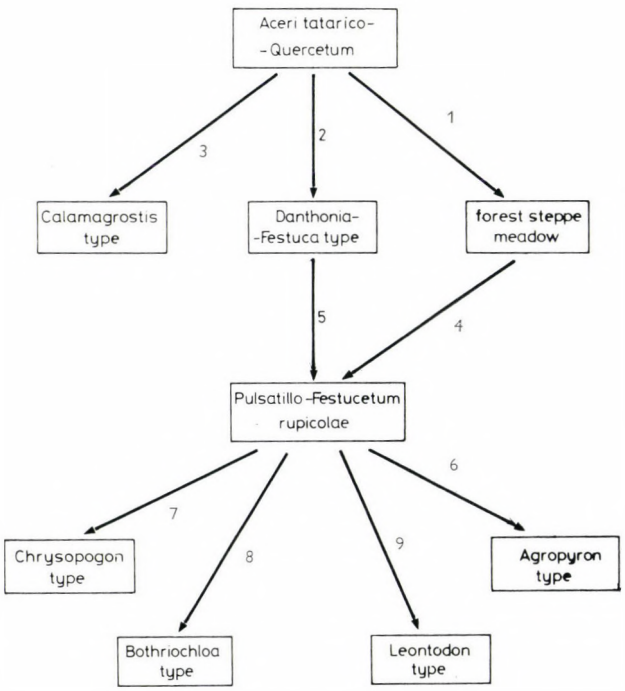

Fig. 2. Hypothetical succession scheme

or less natural type, while at the end a secondary type is found, it is evident that each of the other types can be interpreted as a link in a coenological chain, and between each pair of links there is a successional relation. An alternative conception as opposed to the coenological chain is that the other, intermediate types are mere indications of the inherent heterogeneous character of the vegetation. We ourselves are of the opinion that such an undoubtedly original inhomogeneity is superimposed by an external zoogenic effect and the selective grazing and trampling induces the propagation of several agressive species. We think that the degradation may be multidirectional and the for merely extended subclimax (the moderately grazed species rich slope steppe meadow) was the starting point.

The scheme of the hypothetical retrogressive succession of which certain elements can be recognized in the above discussion of vegetation types is shown in Fig. 2. Comments on the successive stages are as follows:

(1) Forest steppe meadow remnants (on the margin of the former forest steppe to be regarded as climatic climax, and in the clearings of old stands).
(2) Secondary grassland: steppe meadow following the deforestation (*Danthonia-Festuca* type mixed with *F. rupicola* and *F. pseudovina*).
(3) Deforestation vegetation: a permanent state following the deforestation (probably in place of those parts of the former forest which have not turned into steppes). It is based on ample evidence in Hungary; Pál MAGYAR's reports from the Plain are the earliest ones (MAGYAR 1933). In the Northern Hungarian Middle Range (BARÁTH 1963) it indicates the initial developmental stage of the grassland vegetation, in the place of abandoned vineyards often long-lived.
(4) Slope steppe meadow developing after deforestation. Immigration resulting in an enrichment of the vegetation may also have taken place (*Pulsatilla* sp., *Genista tinctoria*, etc.) from the slopes of the Bükk Mountain. At the same time, under the influence of a slight grazing some extent of impoverishment have ensued. In the case of regular grazing *Festuca rupicola*, a species preferred by animals, disappears. *Festuca pseudovina*, on the other hand, matures at a faster rate, sheds its seed earlier—perhaps even before grazed—, and multiplies. Since its tuft senesces more rapidly the animals leave it untouched (BALÁZS 1954).
(5) A process more or less similar to the former one.
(6) *Agropyron repens* dominance. Probably another degradation type of the steppe meadow although it is not out of the question either that it is a remnant of a pioneer stage preceding the steppe meadow (BARÁTH 1963).
(7) Shift of dominance: *Chrysopogon* becomes abundant on somewhat drier hill-sides.
(8) Degradation affecting even the soil: erosion, shallowing of the top-soil (BARÁTH 1963).
(9) Final stage of degradation on the study area.

It is only in comparison to the climatic climax that (2) and (5) are degradation stages, as regards the subclimax they are steps towards a progressive succession. According to CLEMENTS' argumentation *Aceri tatarico-Quercetum*, the forest steppe meadow and *Pulsatillo-Festucetum rupicolae* form a climax unit, while the others (the dominance types) are seral units.

In the sequel the term vegetation type will be alternately used with stage, according to the requirements of the discussion. (The routinely used multivariate analyses if based on the composition will obviously be concerned with the vegetation types; the determination of the stage—the place occupied in the series—has an other criterion.) Beyond that, the following should be noted. Each stage is a vegetation type. On the other hand, for certain vegetation types, namely the remains of the former climatic climax, the forest steppe meadow and even for the stabilized (subclimax) steppe meadow the term stage is used only for the purpose of generalization and for the sake of the scheme. This reservation is decisively motivated by the fact that the units mentioned have also been coenologically determined (they have their

definite places in the coenological hierarchy). The double determination is otherwise a source of confusion. A number of authors, including Hungarians, emphasize the developmental phase character of the vegetation types while placing them at the same time in the formal syntaxonomic hierarchy. That was done, for instance, by BODROGKÖZY (1959) who in the southern part of the Great Hungarian Plain (Kiskunság) studied the degradation phases of lowland *Festuca pseudovina* swards, floristically similar to those we studied, regarding them as facies (*Potentillo-Festucetum pseudovinae poosum bulbosae, cynodonosum, andropogonosum*, etc.). He does not, however, raise the fundamental question (and neither do some other authors): to what extent do the mentioned units satisfy the criteria of the Zürich–Montpellier concept of association in respect of permanence and independent composition? BARÁTH (1963) examines secondary series; the stages replacing abandoned vineyards are mostly regarded by him as subassociations although a stage sometimes lasts only 10–20 years. However, such a rapid change of stages involves a thorough "rearrangement" of the populations, so the permanent composition is also questionable.

The composition

The phytosociological table (Table 1) contains the percentage cover values of the species. A rough qualitative evaluation can be summed up as follows.

About one-third of the species occur in all vegetation types. The four vegetation types at the beginning of the successional series are separated from the second four types by many species (*Dianthus pontederae, Pulsatilla nigricans, Viscaria vulgaris, Teucrium chamaedrys*, etc.), mainly quantitatively: on the basis of either frequency or cover.

The *Danthonia-Festuca* and the *Calamagrostis* type are characterized by a double effect: the influence of the forest steppe meadow and steppe meadow on the one hand, and of the xero-mesophilous meadow on the other. The dominant type-forming grasses do not differentiate absolutely, but their cover values determine one or the other type, or link two or three types. For example *Danthonia-Festuca* type is unambiguously determined by the two nomenclative species, while the *Agropyron* type, apart from *Agropyron repens*, by the high cover value of *Festuca rupicola* and *F. pseudovina*. The types of *Bothriochloa* and *Leontodon* are determined again by the cover values of the two nomenclative species (*Bothriochloa ischaemum* and *Leontodon hispidus*). These two vegetation types at the end of the series are otherwise easier invaded by the meadow species than the former ones, and the abundantly multiplying *Hieracium pilosella* and *Ononis spinosa*, as well as *Prunella lacinata*, a species frequent here, almost appear as separatory species.

The species composition of the vegetation types is characterized by a varying degree of persistence and of extinction of the original forest steppe and steppe meadow species. In general, different mixtures of species of various origin are found in these types. Diagnostic species actually exist in the forest steppe meadow only (these are *Helictotrichon pubescens, Stipa tirsa, Asparagus officinalis, Carex tomentosa, Colchicum autumnale*, and *Peucedanum oreoselinum*).

Species number and diversity

The total number of species per type, the average species number and standard deviation in the quadrats, the CV values and the total cover values are given in Table 2. The total number of species is 99.

It is remarkable that almost every vegetation type has a relatively high total species number. The flora is richest in the forest steppe meadow (75 species), it is thus here that the possibility of different species combinations is the greatest. The lowest number of species (55) is in the *Leontodon* type but it does not mean a poor status of species. The average species number in the forest steppe type is less than half (31) of its total species number, the highest of all, while in all other types this value is slightly higher and almost the same (35).

The order of the CV values of the species number is:

Bothriochloa type 6 < *Agropyron* type 11 < *Leontodon* type 12 < *Chrysopogon*, type 16

forest steppe meadow 16 < *Pulsatillo-Festucetum rupicolae* 18 <

< *Calamagrostis*, type 19 — *Danthonia-Festuca* type 19

So the CV values decrease in accordance with the extent of degradation, while the most variable are the *Calamagrostis* and *Danthonia-Festuca* types at the starting point of the series. The total cover is very similar in all the eight types; in the forest steppe meadow and in the *Calamagrostis* and *Danthonia-Festuca* types the total cover value represents the joint cover of all species, while in the degraded types it is added up mostly by a few dominant species. The final stage poor in species shows the lowest value even of total cover.

Diversity was calculated for all quadrats on the basis of the SHANNON formula, while the value of evenness was determined after HURLBERT (1971):

$$\text{Evenness} = \frac{H - H_{\min}}{H_{\max} - H_{\min}}$$

Trend of change of average diversity values:

Pulsatillo-Festucetum rupicolae, forest steppe meadow, *Chrysopogon* type >

> *Calamagrostis* type, *Danthonia-Festuca* type > *Agropyron* type, *Bothriochloa* and *Leontodon* type

Both in the *Pulsatillo-Festucetum* and in the *Agropyron* type the average species number is low; the highest diversity value observed in the former can

Table 1

Phytosociological

Name of vegetation-types	A					B					C				
	Calamagrostis epigeios type					*Danthonia-Festuca* type					Forest steppe meadow				
Numbering of sample quadrats	16	17	18	19	20	6	7	8	9	10	36	37	38	39	40
Agrostis tenuis	2	20	4	10	20	7	10	5		15	3	5	10	8	10
Filipendula vulgaris	15	5	12	10	4	3	5	5	3		10	15	20	20	10
Carex caryophyllea	8	8	3	7		7	5	2	8	2				5	3
Seseli annuum	1	1	2	4	3	2	10	5	8	2				10	3
Plantago media	1	3		3	1		3	2	2	2	1	5	15	15	
Anthoxanthum odoratum	1	2		1	1		2	2	2	8				2	5
Luzula campestris	3	3	2	3		3	5	3	4	2		1		5	5
Achillea pannonica	1	1	1	1	1	2	3	5	8	5	1	1	2	3	3
Thymus marschallianus	2	2	3	2		2	2	4	5	2	5	5	10	5	2
Genista tinctoria	2	4	1	3	3	1	3	3	2	2					1
Koeleria cristata	1							10		1		2			2
Inula britannica										1		1	4	3	
Asperula cynanchica	13		1	5	2	1	2	3	2	2			3	3	5
Eryngium campestre	3			12	2	2	1	2		1	2	2	2	3	5
Pimpinella saxifraga	15		1	15	2	2	3	2	1	2		1	3	3	5
Euphorbia cyparissias	1	1	2		2	2	1	2	3	2	2	1			
Plantago lanceolata	3	1	1	1	1	3	1	2		2	2	2	2	3	o
Trifolium montanum	3		1	1	1	5	2	2		2					
Carlina vulgaris	1	1				1			2						1
Hypericum perforatum	1	2	2			1	1	2	3	1	1	3			
Veronica spicata	1	2	2		1		1	1	2	1				2	
Hieracium bauhini	2			1			2			1		3		3	3
Scabiosa ochroleuca		2	1	3		1				1		1		1	
Dorycnium herbaceum											5	2			
Fragaria viridis	2	1	8			1				1	5	5	5		2
Verbascum phoeniceum			1		2	1		2		2	5	10			5
Hieracium pilosella	1	1				1	2	2		2	3				
Potentilla arenaria		1					5	2	3	3		1			
Plantago stepposa															10
Senecio jacobaea											1				
Lolium perenne															
Daucus carota												2			
Crepis sp.				1	2						1				
Vicia sp.				1	2						1				
Viola sp.															
Bromus mollis															
Ajuga genevensis															
Crataegus monogyna														3	
Scorzonera purpurea	1													2	2
Rhinanthus minor															
Colchicum autumnale													1		
Thalictrum minus										2			1		
Helianthemum ovatum		5								5					
Helictotrichon pubescens															5
Peucedanum oreoselinum															1
Helictotrichon pratense									1	5					10
Stipa tirsa										15					
Salvia pratensis				8						2				5	15
Phleum phleoides											10	3			
Carex tomentosa											20	10			
Silene otites											2	5			
Silene parviflora												5			
Allium sphaerocephalum													1		
Agrimonia eupatoria												1			

table

D					E					F					G					H				
Pulsatillo-Festucetum r.					Agropyron type					Chrysopogon type					Bothriochloa type					Leontodon type				
31	32	33	34	35	26	27	28	29	30	21	22	23	24	25	1	2	3	4	5	11	12	13	14	15
3	2	8	9	8	3	5	5	5	8	15	8	10	10	10	15	5	20	5	7	7	12	8	2	3
1			7	2	8	8	5	10	8	5	3	15	10	10	4		1	5	2	1	2	1	2	
1		10	7	1	5	3	10	30	15	20	15	5	10	20	8	3	5	5	8	25	5	15	20	10
1			5	2	2	30	15	15	15	5	5	5	15	5	5	4	15	10	5	1	3	3	10	5
			2			10	3	15	3		5				3	3	10	10	8	3	5	7	5	
6	4	9	1	10	3	2	2	3	2	3		3	15	2			3	15	5	5		5	5	
8	4	4	4	6	2	8	10	5	3	5	3	5	3	5	2	2	2	2	4	1	1	1		
10	5	6	5	7		1	8	5	3	5	2	3	8	2	3	2	2	2	2	2	5		3	5
12	20	10	5	9	4	2	3	5	5	5	3	5	10	3	5	2	2	2	2	3	2		3	2
3	3	3	3	4	2	3	3	2	5	3	10	5		1	3	2	2	3	1		1		3	2
		1				1		1	1	1	2	3		1			3						1	
								4			2	4	3			1	2							
	1	1				10	5	5	2	3	2	2		2	2	3	3		2			1	1	1
1		1	1	3		3	2	3		3	7	3	2	2	8	1	5	2	3	3	5	2	2	3
			1				1	1	2				1	2	1	1	1	3	2		1	3	2	2
2	2	2		2	2	1	2	5	3	2		2	1				2		2	1		1	1	1
1	4		1	1	2	2		3		2				1	1	1	2	1						
						2		10		3		7	3	2		1	1				1	1	2	
1	2	1	1		2				1	3	4	3	1	3	2	2		1	3		1	2		3
1		1		1	2	1	3	2	1		3	3	2	2	1		2							
1			1	1	2			2			2	2	1		2	1	1	2	1		1	1	1	1
1	2		1	2		1	1	3	2	2	1	2	3	2	2				1	5				1
	3	1	1	1	3	1			1	2	1	1		1	1			1	1	1				
										1		2	1	3										
		2	4		5	3	3	2	2		3	3			1		1			1			1	1
2			1	2	5		1	1	2	2	8	5	1	2	2								1	
2	2	2	1	2		2				20	10	15	5	10	5	5	2	3	3	5	5	5	8	7
2	5	2	1	2	1		1		1	5	15	10			1					3	1	1	2	3
					15						5													
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											2						1							

continued

Name of vegetation-types	A					B					C				
	Calamagrostis epigeios type					*Danthonia-Festuca* type					Forest steppe meadow				
Numbering of sample quadrats	16	17	18	19	20	6	7	8	9	10	36	37	38	39	40
Veronica serpyllifolia													1		
Convolvulus arvensis										1			1		
Veronica dentata													1		
Dianthus pontederae	3		2			1		3					5	5	5
Pulsatilla nigricans	5		8				1	1	10	2			5		10
Rumex acetosella								1	1						
Teucrium chamaedrys			10												
Viscaria vulgaris			1								1				
Poa angustifolia								5							
Falcaria vulgaris				2		2						1			
Galium verum			1		3			2				1			5
Seseli varium						10							2		
Centaurium erythraea															
Thesium ramosum							1				1				
Trifolium arvense															
Trifolium ochroleucum															
Alopecurus pratensis														1	2
Ononis spinosa	5														
Cerastium sp.		1		1	1	1			1	1					1
Linum catharticum		1			2	1				1					
Euphrasia tatarica		1					1	1							
Polygala comosa			1	1		1	1		1	1					
Trifolium campestre		1			1			1							
Prunella laciniata	1						1			2					
Trifolium pratense	1	1			1		1			1					
Briza media		8	5		7										3
Danthonia decumbens	1	2	3		10	3				1					1
Centaurea pannonica	1	2			4		2								
Viola arenaria	1	5	2		5	2	2			1					
Lotus corniculatus				5	8	1		1		2	1				
Campanula rotundifolia	5				2				1					1	
Stellaria graminea	3		2	1	1	1							2		
Trifolium alpestre		1	20	45				2			2	5		1	3
Calamagrostis epigeios	70	60	55	50	45										
Chrysopogon gryllus											8			5	
Agropyron repens				1				3					10	10	5
Festuca rup. et ps.	20		15	20	10	60	35	80	30	20	35	80	75	90	30
Danthonica alpina	1		10			20	40	20	30	50				2	40
Bothriochloa ischaemum	1		1	1		10		8	3	4	3	15		5	
Leontodon hispidus	8	8	8	8	15	3	25	7	10	4	1		1	3	3

be explained with the low total cover and the even distribution of cover values, while in the latter with the high total cover and the possibly related lower evenness.

Trend of change of average evenness values:

Pulsatillo-Festucetum rupicolae > forest steppe meadow, *Chrysopogon* type > *Calamagrostis* type, *Danthonia-Festuca* type > *Agropyron* type > *Botriochloa* and *Leontodon* type

table 1

D					E						F				G					H				
Pulsatillo-Festucetum r.					Agropyron type						Chrysopogon type				Bothriochloa type					Leontodon type				
31	32	33	34	35	26	27	28	29	30	21	22	23	24	25	1	2	3	4	5	11	12	13	14	15
						1			1															
2	1	3	1	1				1											1					
1	1	1	2	3																				
2	4	1	1	1								1			2									
1		4																						
7		6	1	4																				
																				1				
					2	2										2				3				
					2	3							3			1	1		2	1				
																				4				
												1			1			2		1	1			
												2						2	1					
												1				1			1					
																			2	1			1	
															3	10								
												3				10		2	2	1		7	1	1
			1				1		1		1	1			1	2	1	2	1	1		1		
												1		3	1	2	1	1	1			1		
	1		1		1	1				1	1	1	2	1	2	1	1	1		2	1	1	1	1
					1	1		1	1	1		1	2	1	2	1	1	2	2	1	1		1	
									1		1	3			1	1	1	1	1	1	1		1	1
																2	1	2	1	1	2		1	1
									1				3	3	2			3	5			2		1
			1							1	2			20	5			3		3	3	2	1	5
	1	2																		1				
1			2							1														
											3						2			1	2		1	
					4						1	2						1		1	1			
							15		10					2				2		1		2	1	2
									3	70	75	60	75	60			3	2	3			4		
					70	80	80	70	80		10													
17	28	12	7	14	60	40	50	40	20	15	15	30	25	30	15	10	15		10	12	5	5	5	8
			3		3	2	3	2	2				5		5	5		15	10	1	1	1		3
4	2	3	3	5		1	5			5	3	4	3	3	50	60	50	70	80	50	10	20	25	8
4	1	3	10	4	1	3	1	8	2	8	5		2	5	12	25	3	30	25	4	60	45	35	60

The lowest evenness is shown by the final stages of degradation. The differences are not, however, great either in evenness (0.61–0.77) and diversity (2.46–2.9), or in average species number and total cover.

Extent of "self-reproduction", coordination

The degree of organization of a vegetation type may also be referred to by an index which somehow expresses the "perfectness" of the "self-reproduction", the ability of forming true copies recurring from stand to

Table 2

Species number and diversity

Vegetation type	Total number of species	Average number of species	CV %	Mean of total cover	Mean diversity ($\bar{H}$)	Mean evenness ($\bar{V}$)
Calamagrostis epigeios type	62	35 ± 2.8	19	190	2.70	0.658
Danthonia-Festuca type	61	35 ± 2.9	19	174	2.70	0.656
Forest steppe meadow	75	31 ± 2	16	196	2.73	0.722
Pulsatillo-Festucetum rupicolae	44	28 ± 2	18	99	2.90	0.776
Agropyron type	53	31 ± 1.5	11	235	2.46	0.640
Chrysopogon type	59	35 ± 2	16	228	2.80	0.718
Bothriochloa type	62	36 ± 0.9	6	192	2.68	0.636
Leontodon type	55	33 ± 1.8	12	152	2.61	0.618

Table 3

The averages of correlation coefficients among five replicate plots in eight vegetation types

Vegetation type	$\bar{r}$	CV %	$\bar{r}'$	CV %
Calamagrostis epigeios type	0.8043 ± 0.02	11.41	0.4003 ± 0.02	18.09
Danthonia-Festuca type	0.7767 ± 0.04	16.31	0.5132 ± 0.02	15.06
Forest steppe meadow	0.7080 ± 0.06	30.69	0.2287 ± 0.04	60.47
Pulsatillo-Festucetum rupicolae	0.7298 ± 0.04	20.27	0.6547 ± 0.01	11.43
Agropyron type	0.9134 ± 0.01	3.82	0.5645 ± 0.03	18.88
Chrysopogon type	0.9138 ± 0.05	2.01	0.5584 ± 0.02	14.42
Bothriochloa type	0.9060 ± 0.01	5.54	0.5272 ± 0.03	16.45
Leontodon type	0.7070 ± 0.08	39.34	0.5283 ± 0.02	12.76

$\bar{r}$ = BRAVAIS' correlation coefficient; $\bar{r}'$ = coefficient obtained from the χ^2 values.

stand (JUHÁSZ-NAGY and VIDA 1978). We therefore examined the common occurrence of species within a type to see how much the repetitions were similar concerning the cover relations among species. In all possible pairwise combinations of five repetitions we calculated the correlation coefficients (r') from the χ^2 values, as well as the BRAVAIS's correlation coefficients on the basis of the cover values, then determined their average value and the standard deviation of data (Table 3).

The r' values obtained from the χ^2 coefficients are relatively low. In the case of the forest steppe meadow the $\bar{r}'$ value (0.23) is particularly low and the CV value is very high.

The correlation coefficients calculated on the basis of cover are high in all types. The highest $\bar{r}$ and the lowest CV values were obtained in the three derived types (*Agropyron*, *Chrysopogon*, *Bothriochloa* types). The other extreme is represented by the forest steppe meadow and the *Leontodon* type where $\bar{r}$ (0.7) is the lowest and the CV value (30–40%) is the highest. In the forest steppe type this heterogeneity is caused by the large number of low frequency (and low cover) species occurring accidentally, while in the *Leontodon* type it is due to the diversified cover distribution of species within a total species number much smaller than in the former type. The relatively low degree of coordination of the forest steppe meadow may be an inherent feature, while that of the *Leontodon* type probably reflects distortions caused by grazing, too.

Similarity, grouping

Multivariate analyses

In surveying the subjective, visually constructed vegetation types multivariate analyses (classification and ordination methods) were used that made possible to study the types with all species taken into consideration by extracting the information in the data.

Data for multivariate analyses

The multivariate data set is consisted of presence and absence, as well as cover values estimated for 99 species in 40 plots.

Further on we are giving in every case results calculated from raw data. Similarities obtained from transformed and standardized data gave less interpretable results for the very reason of making the data matrices uniform. We made the very differences, namely those in the frequency of species and in the cover values, disappear which in the given situation, in particular with vegetation types differentiated by cover distribution may be of great importance.

The total data set was subjected to divisive information analysis (Lance and Williams 1968) using presence-absence data, to different clustering methods using both binary and cover data and to principal component analysis (PCA) of the correlation matrix calculated from the raw cover data.

Computer programs ASSINF, NCLAS and PRINCOMP written by Podani were used to run the classification and ordination analyses. (The description of computer programs excluding PRINCOMP are found in Podani 1980.)

Association analysis

The result of classifying the full data set with the divisive information analysis (LANCE and WILLIAMS 1968) where the divisive parameter is the reduction of information content, "information fall", is shown in Fig. 3 with references to the number of quadrats taken in each division.

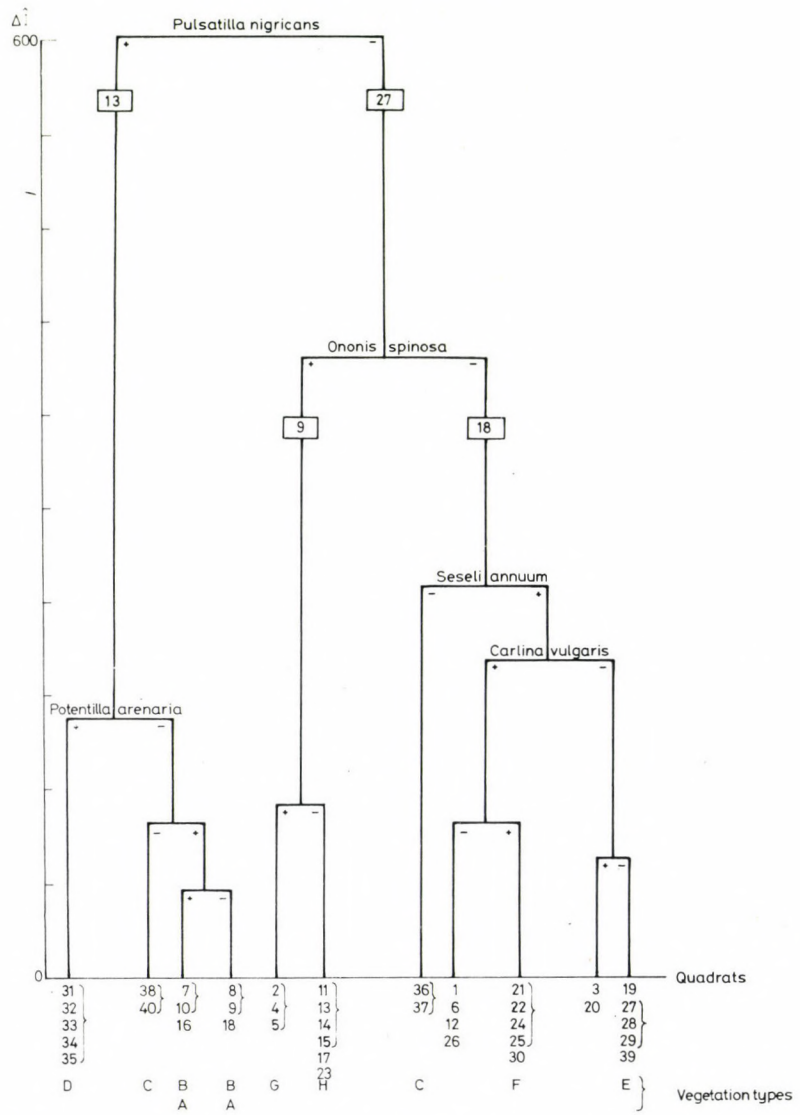

Fig. 3. Hierarchy for quadrats (see in Table 1) obtained with the LANCE and WILLIAMS (1968) version of association analysis

The first division separates two large groups based on *Pulsatilla nigricans*. One of them in which this species occurred contains five quadrats of *Pulsatillo-Festucetum rupicolae* as well as the quadrats of those three types from which it may have been derived (Fig. 1). The other large group where *Pulsatilla* (the low tolerance nomenclative species of the steppe meadow) is absent is represented by degraded stages of the slope steppe meadow. In this latter group *Ononis spinosa* is responsible for the next division. It is a very agressively spreading weed species, and the fact that it still separates the degraded stages suggests that intermediate degradation stages may also exist there. At the ecological interpretation of further divisive species we do not even make an attempt, as it can be supposed that species may be absent from certain quadrats by chance (misclassification). For the same reason types represented by at least three quadrats in a cluster are marked in Fig. 3.

Agglomerative clustering methods

The possibility of misclassification is much lower with the agglomerative clustering methods, especially when, as in our case, there is a data set expressing the cover relations.

The clustering methods chosen all belong to the polythetic, route optimizing hierarchical methods. The sorting algorithms used are furthest neighbour (complete linkage) and sum of squares agglomeration (WARD's method).

The similarity matrices were calculated based on the following resemblance functions:

Cover data	Presence-absence (binary) data
1. Euclidean distance	Euclidean distance
2. Product moment correlation coefficient	r' calculated from χ^2
3. CZEKANOWSKI's percentage similarity	SØRENSEN index
4. WISHART's similarity ratio	JACCARD coefficient
5. —	Weighted dissimilarity index = WDI (PODANI (1978)

In the case of the vegetation types examined the value of the correlation coefficient is reliable, because the common and absent species do not extremely differ in number. Undistorted results are given by the SØRENSEN and JACCARD indices, too, since the species numbers of our object compared are nearly the same. With WDI (when weighting is carried out with the probability of occurrence) quadrats of higher species number and the frequent species are more decisive than the species poor plots and rare species.

Dendrograms using various quantitative indices can be said to be very similar, almost identical concerning their overall structure.

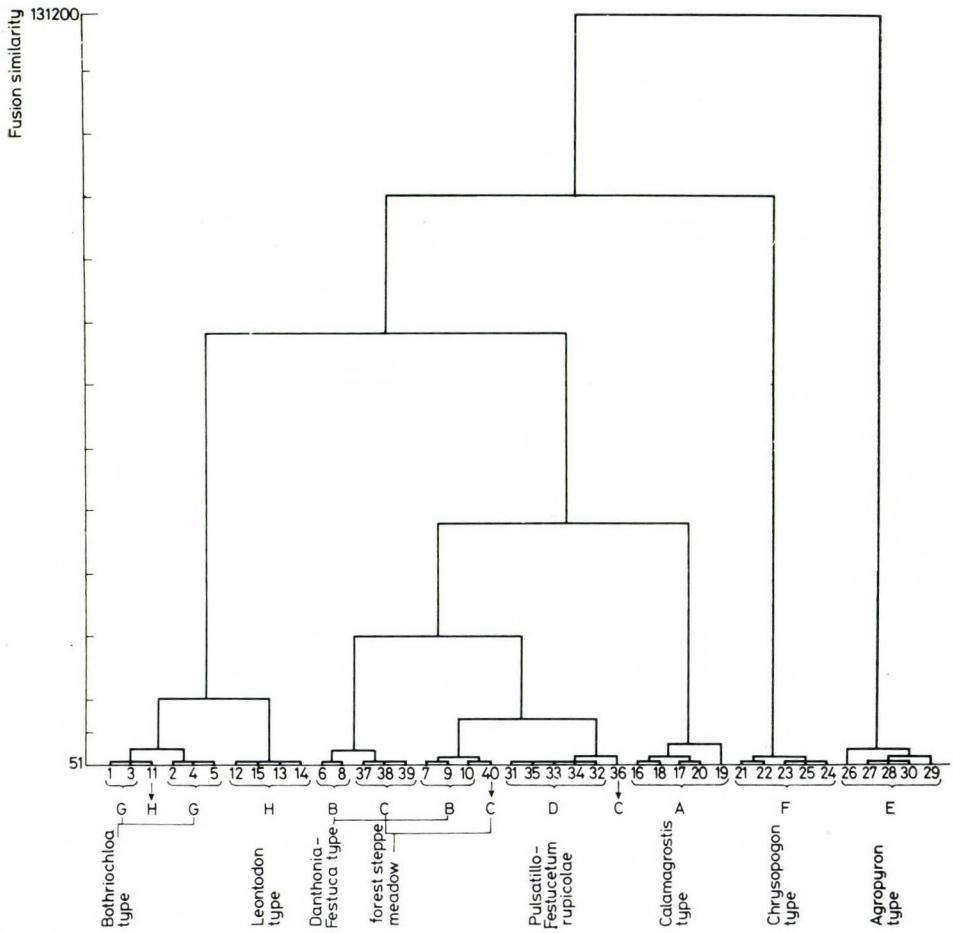

Fig. 4. Hierarchy for quadrats (based on the Euclidean distances from cover raw data)

At a very low similarity level all analyses mostly differentiate 7 highly discrete groups. Depending on what similarity level (10–40%) is regarded arbitrarily as a partitioning line, only 5–6 sharply discrete clusters may occasionally be observed (Figs. 4–7).

The *Danthonia-Festuca* type is almost the only one where the replicate plots are separated (in a group of three and a group of two). Similarly in the case of fusions calculated from various indices on the basis of the complete linkage sorting strategy the forest steppe meadow is also divided up (3–2 and 4–1, respectively). The main point is that at the highest similarity level the *Danthonia-Festuca* type is linked always with the forest steppe meadow, and

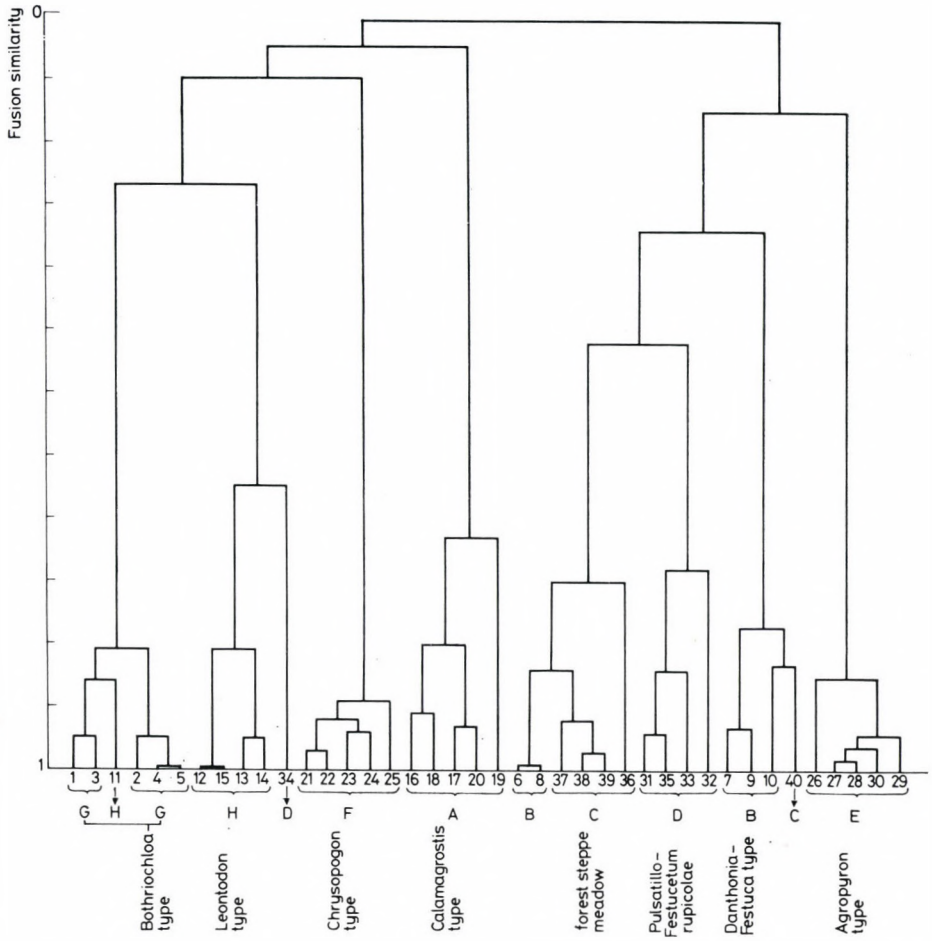

Fig. 5. Hierarchy for quadrats (based on the product moment corr. coeff. from cover raw data)

at a lower level they are joined with the *Pulsatillo-Festucetum rupicolae*. However, the latter may form a completely independent relatively homogeneous cluster (Figs. 5, 6, 7).

The second most similar pair among the fusions is formed by the *Bothriochloa* and the *Leontodon* type, though at a certain level they also show high independence (Fig. 6). The *Calamagrostis*, *Agropyron* and *Chrysopogon* types, on the other hand, form clusters well isolated both from all the other types and one another.

The similarity levels give information on the internal homogeneity of clusters. The most homogeneous groups were obtained in case of the *Agropyron* and *Chrysopogon* types, the 5 sampling units are at the smallest distance from one another in each group regardless of clustering algorithm. The

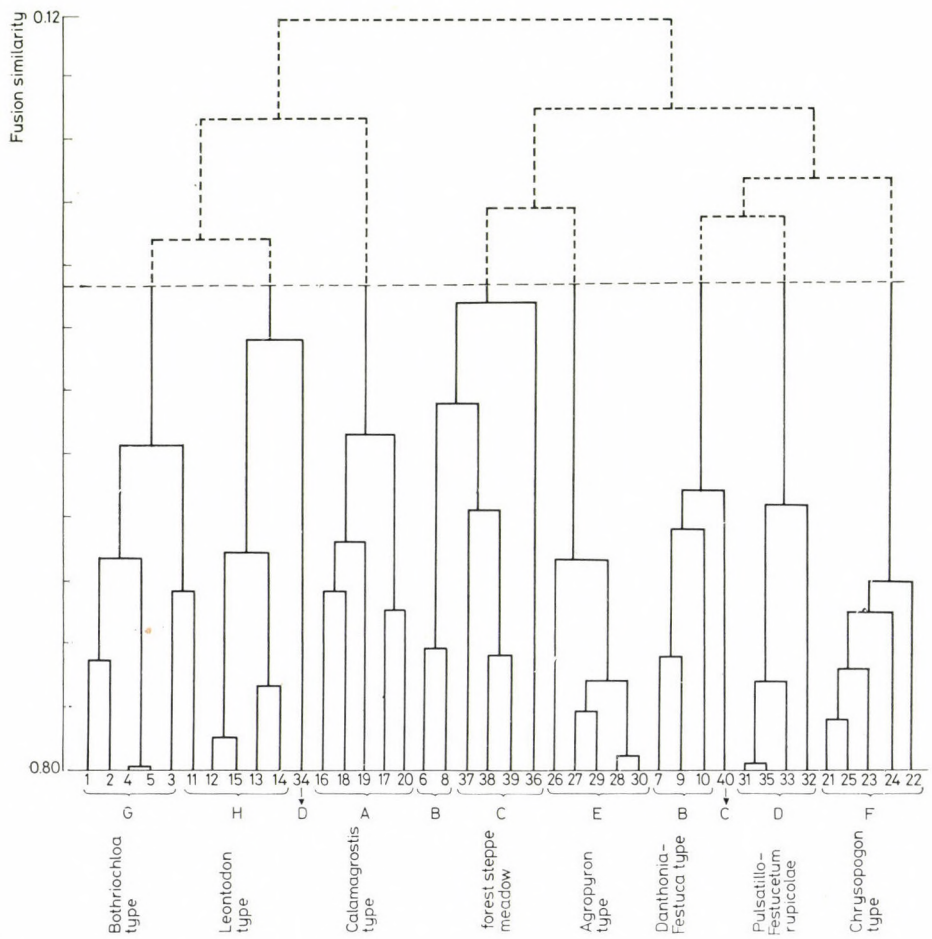

Fig. 6. Hierarchy for quadrats (based on the CZEKANOWSKI's percentage similarity)

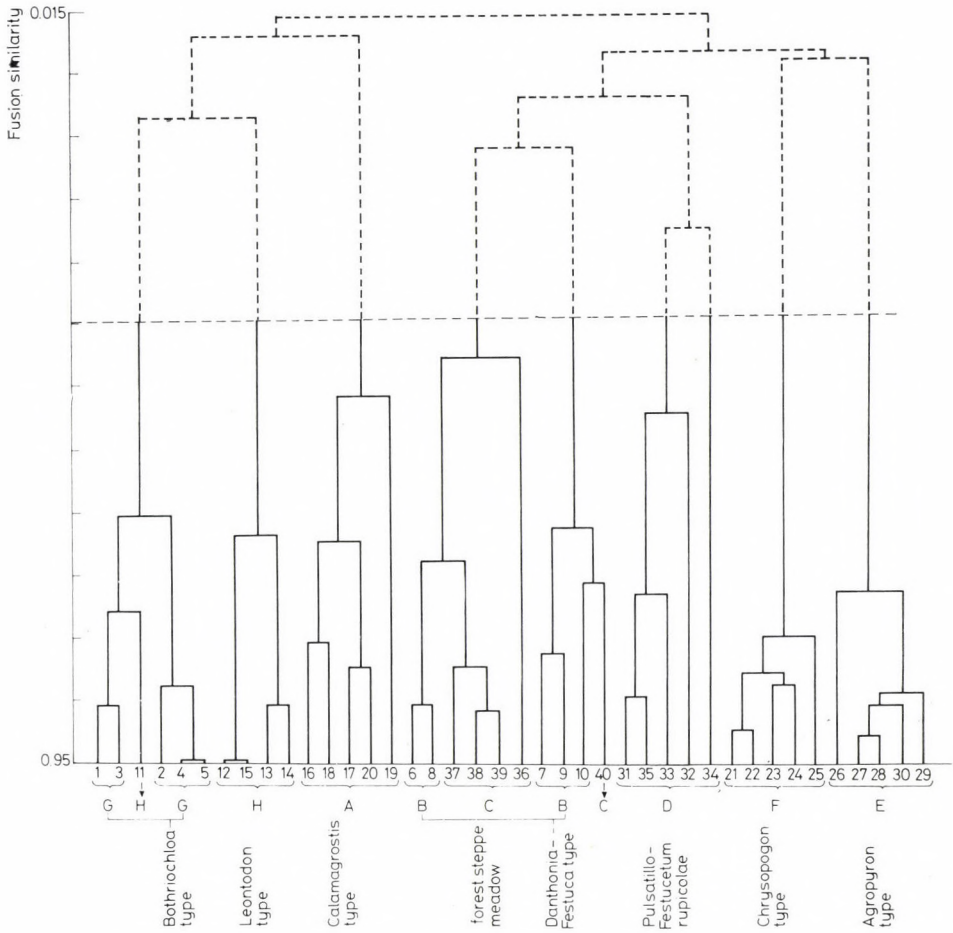

Fig. 7. Hierarchy for quadrats (based on the WISHART's similarity ratio from cover raw data)

clusters of the *Bothriochloa* and *Leontodon* types are also fairly homogeneous, while the most heterogeneous clusters were obtained in case of the forest steppe meadow, the *Calamagrostis* and the *Danthonia-Festuca* types. The interpretation of these results will be given later.

In case of binary data (Figs. 8–12) the cluster analysis, as expected, resulted in more heterogeneous clusters than when similarities were examined on the basis of cover data. The similarities between the clusters were also lower.

However, it is remarkable that on the basis of the presence and absence of species identical results were often obtained contrary to those based on quantitative data. The common features of methods starting with the calculation of binary indices (1–3.) are: The most homogeneous clusters comprise the

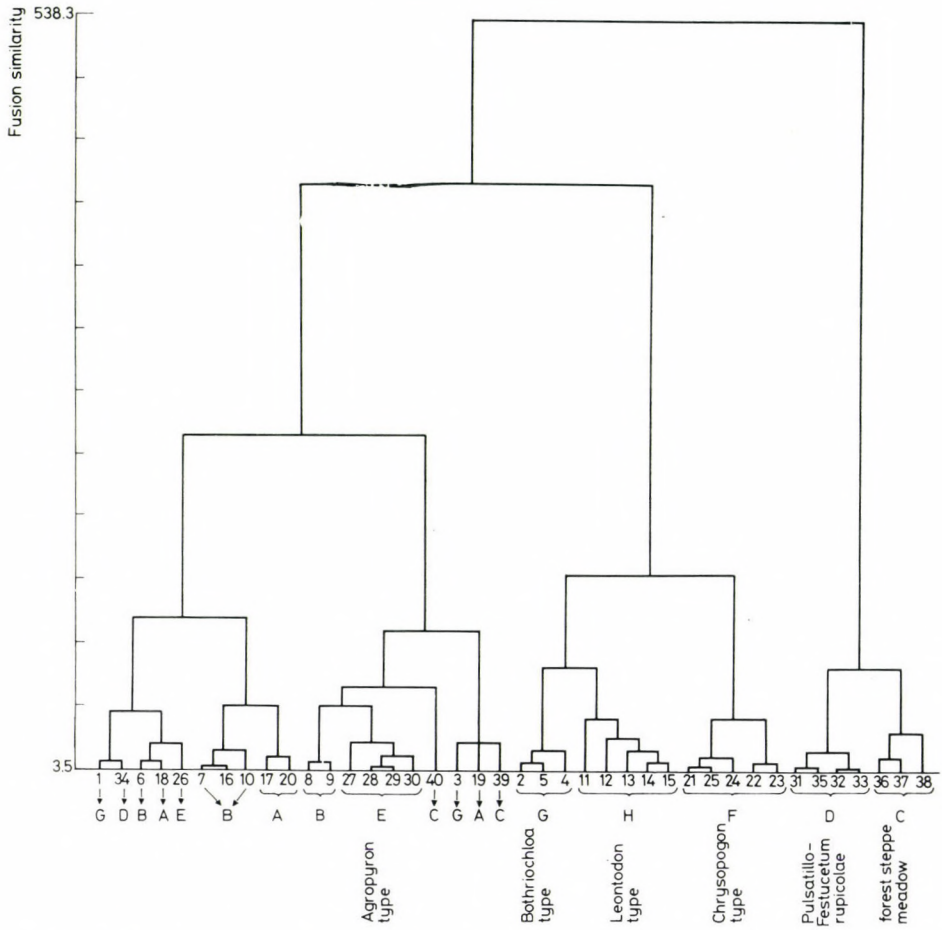

Fig. 8. Hierarchy for quadrats (based on the Euclidean distances from binary data)

Chrysopogon and *Agropyron* types. Similar are *Pulsatillo-Festucetum rupicolae* and the *Leontodon* type of which always 4–5 quadrats are assigned together by the sorting strategy.

The *Danthonia-Festuca* type is in each case highly disorganized forming no separate unit whatsoever.

In the case of the forest steppe meadow only 3 quadrats are always similar at a higher level, but they form in every case a totally isolated independent cluster.

Differences: The *Calamagrostis* type never occurs as a perfectly uniform cluster, the 5 sampling units are in most cases completely separated from one another (1–5), though less so than in the *Danthonia-Festuca* type.

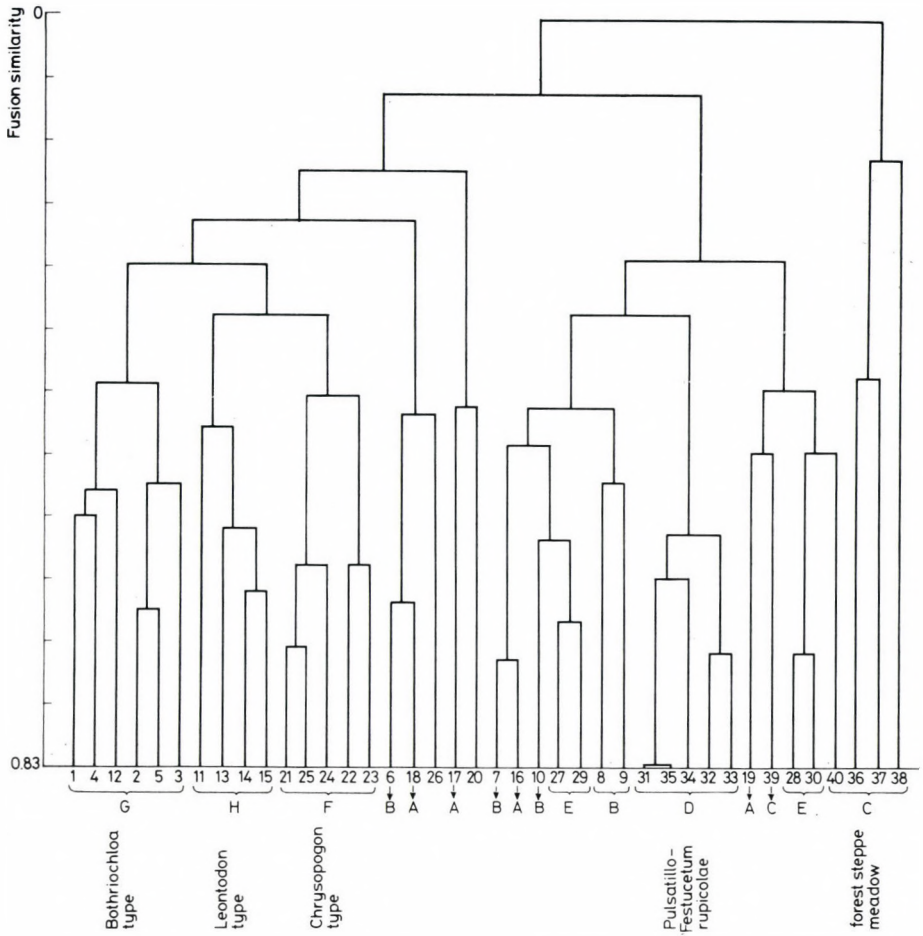

Fig. 9. Hierarchy for quadrats [based on the correlation coefficients (r') from binary data]

The *Bothriochloa* type, with the exception of clusters calculated from the χ^2 values forms in each case a relatively homogeneous cluster containing only 3 replicate plots and only on the basis of Euclidean distance and SØRENSEN index comes it close to the *Leontodon* type at a low fusion level.

The *Agropyron* type in one case (χ^2) does not form homogeneous cluster.

WDI, the only weighted binary index among the functions applied give varying results compared to the former ones. The quadrats of the *Danthonia-Festuca* type greatly differ here, too, and the other types also form rather heterogeneous clusters, except the forest steppe meadow and steppe meadow. At the top level two large groups can be distinguished; this sorting completely agrees with the first division obtained by association analysis.

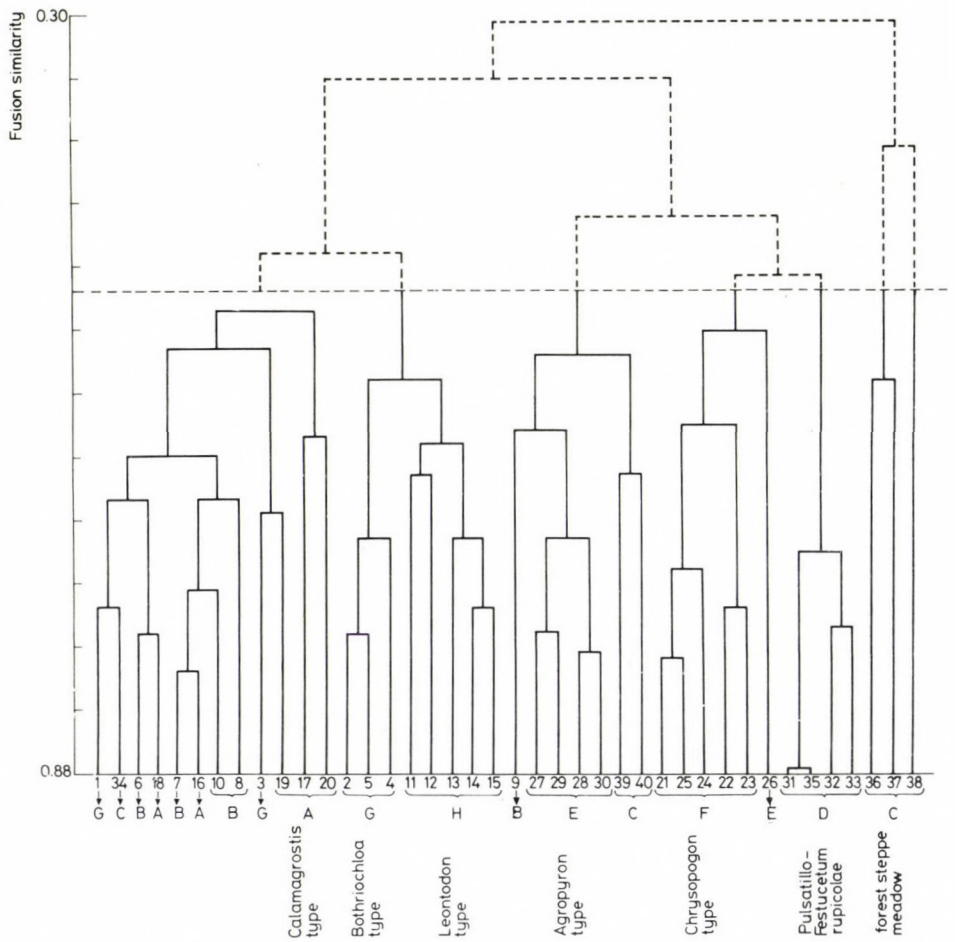

Fig. 10. Hierarchy for quadrats (based on the SØRENSEN index from binary data)

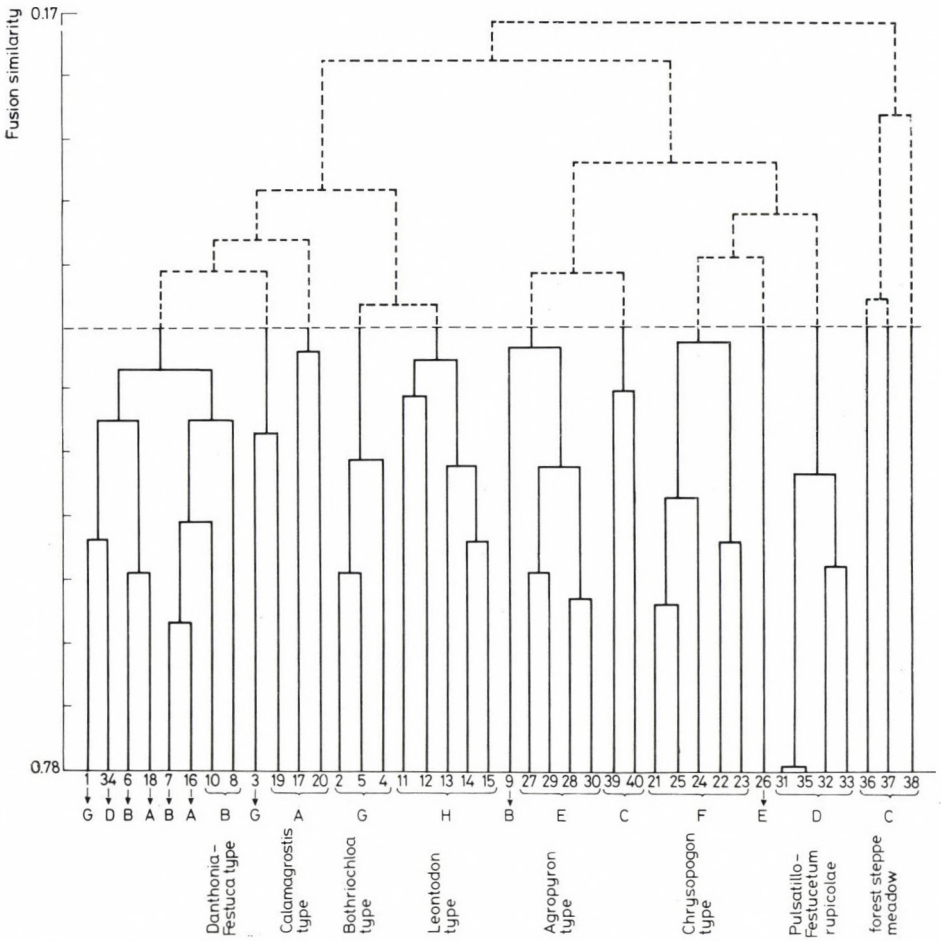

Fig. 11. Hierarchy for quadrats (based on the JACCARD coefficient from binary data)

On the basis of the above findings besides the *Danthonia-Festuca* type the *Calamagrostis* type does not also seem a well-defined (uniform) category.

From the foregoing we have got a rather convincing picture on the similarity among the eight vegetation types. So far the 40 quadrats have been separately treated so as to obtain information on the variability of the samples. Since the standard deviation of the similarity values between the replications is low, it seems reasonable to calculate the average of similarity values in order to make the picture clearer.

On the basis of the correlation coefficients and Euclidean distance, if groups fused at a lower the arbitrary 40% similarity level are left out of consideration, five large groups can be distinguished. These are: 1. *Bothriochloa*

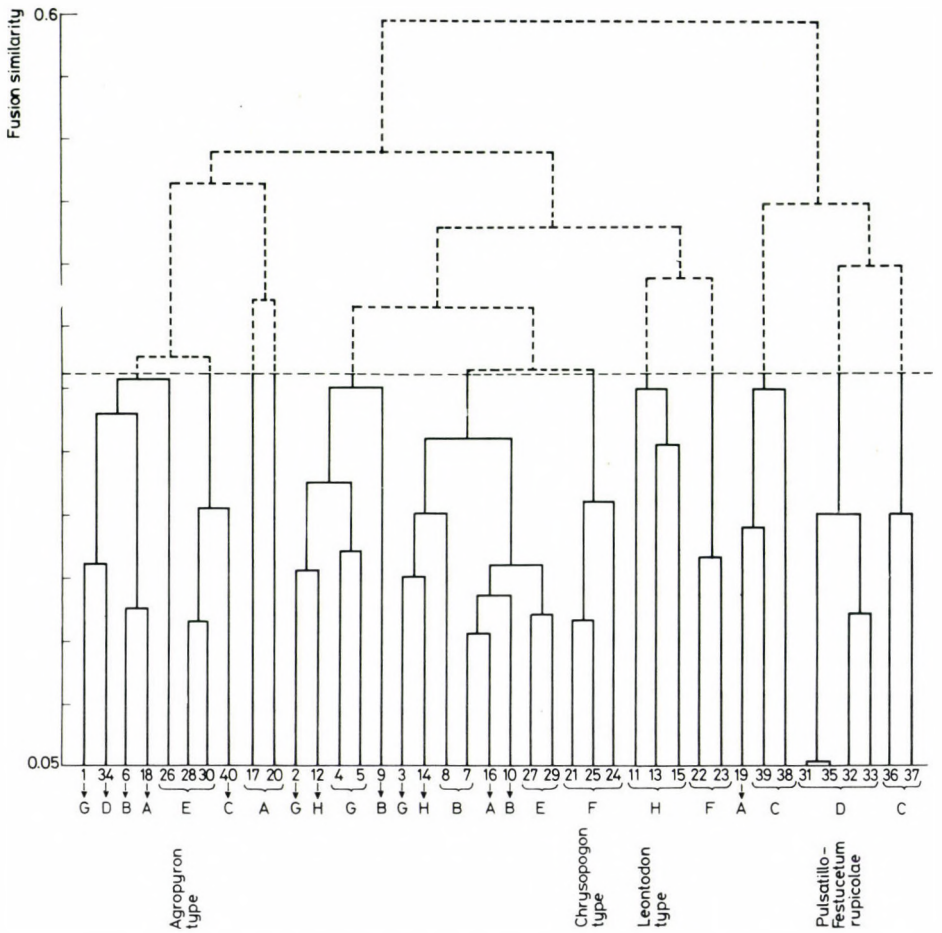

Fig. 12. Hierarchy for quadrats (based on the *WDI* from binary data)

and *Leontodon* type, 2. *Pulsatillo-Festucetum*, plus the forest steppe meadow and the *Danthonia-Festuca* types (from which the first group may have been derived), 3. *Agropyron*, 4. *Chrysopogon*, 5. *Calamagrostis* types, as independent units. It can be seen that the fusion levels did not change at regular intervals (Figs. 13, 14).

The cluster obtained from the binary data ($\chi^2 - r'$), furthest neighbour sorting show a picture different from the former classifications. The similarity levels at which types are fused are relatively low, and only 4 groups can be distinguished (Fig. 15). The *Calamagrostis* type and the forest steppe meadow form separate groups, while *Pulsatillo-Festucetum rupicolae*, *Danthonia-Festuca* and the *Agropyron* types comprise another group, as well as the *Bothriochloa-Leontodon-Chrysopogon* types.

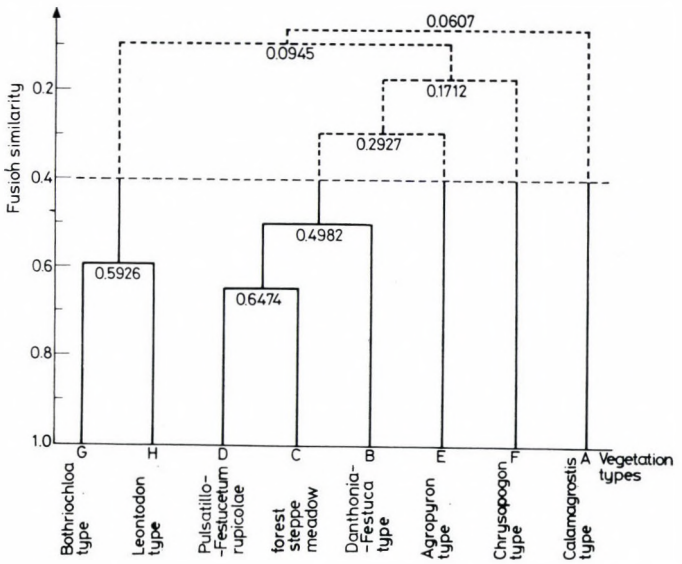

Fig. 13. Dendrogram (based on the product moment corr. coeff.) indicating hierarchy for vegetation types in Table 1

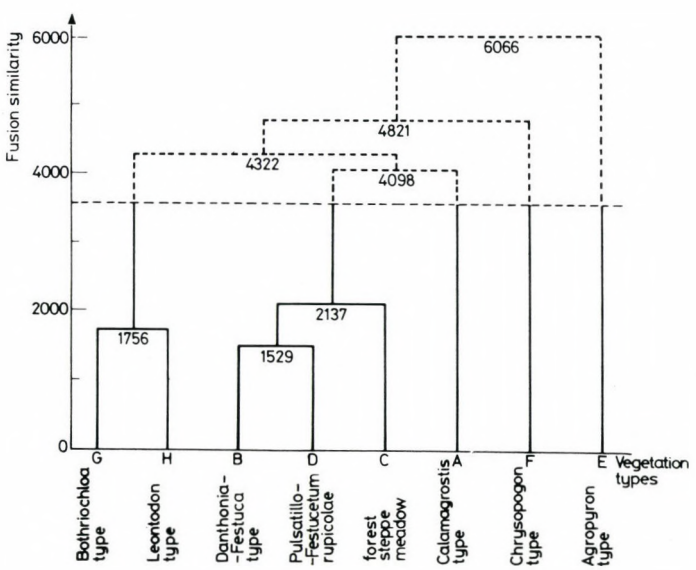

Fig. 14. Dendrogram (based on the Euclidean distances) indicating hierarchy for vegetation types in Table 1

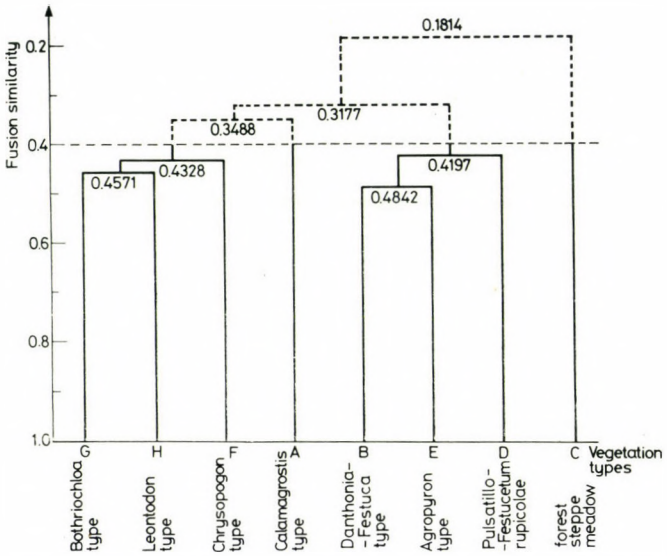

Fig. 15. Dendrogram (based on the r') indicating hierarchy for vegetation types in Table 1

Principal component analysis

The clustering methods are known to be liable to overemphasize the discontinuity of vegetation; they may force a separation into discrete classes even if the vegetation is continuous otherwise. Owing to this disadvantage it is advisable to use ordination methods which may confirm the results of classification. Besides showing the relations between the sample plots on the basis of their arrangement in the Euclidean space, they may give information on factors determining the species composition and on vegetational gradients.

It can be seen (Figs. 16, 17) that the eight vegetation types studied are rather well separated in the two- and three-dimensional space (the result of *PCA* is shown on the basis of the first three principal components). Thus, sufficient agreement with the clustering methods has been obtained, the discontinuity between types is justified by *PCA*.

One extreme in the diagram (IInd axis) represents the *Bothriochloa* and *Leontodon* types, the two final stages of the degradation series and the other corresponds to the vegetation types at the beginning of the series. The other extremely positioned pair is the compact and fairly discrete groups of the *Calamagrostis* and *Chrysopogon* types (IIIrd axis). The arrangement along the axes may suggest two kinds of trend. It is remarkable that axis I arranges hardly if at all. All the more does axis II so; it can be interpreted as a succes-

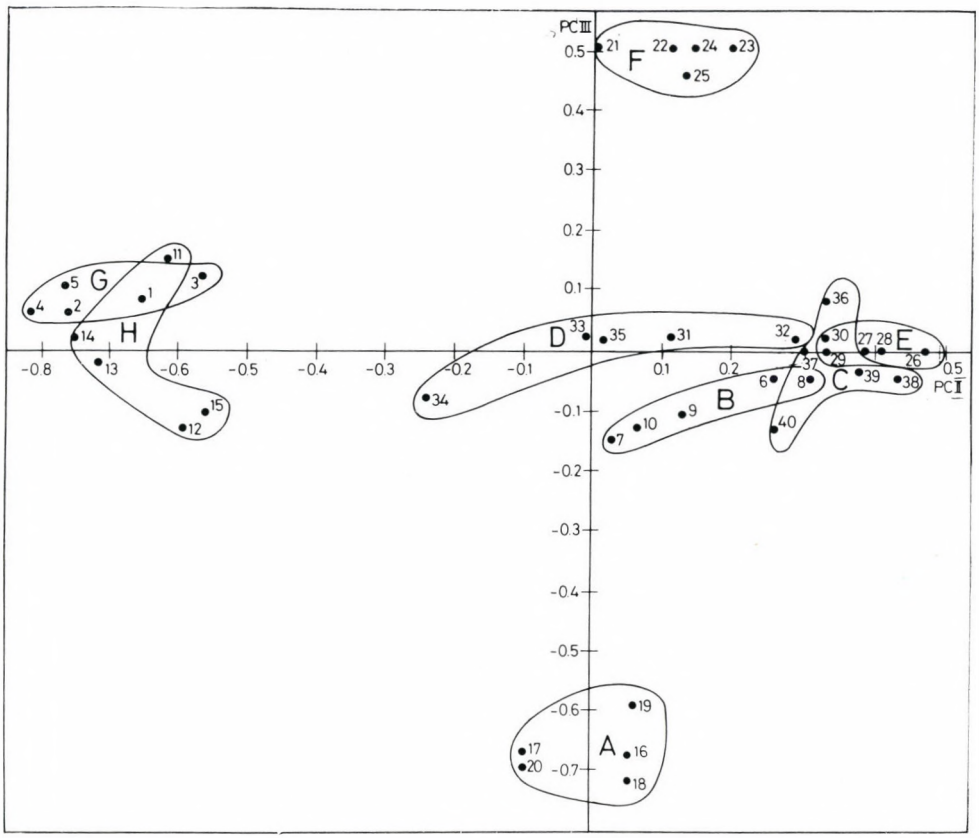

Fig. 16. Ordination of sampling plots with the 2nd and 3rd principal components axes

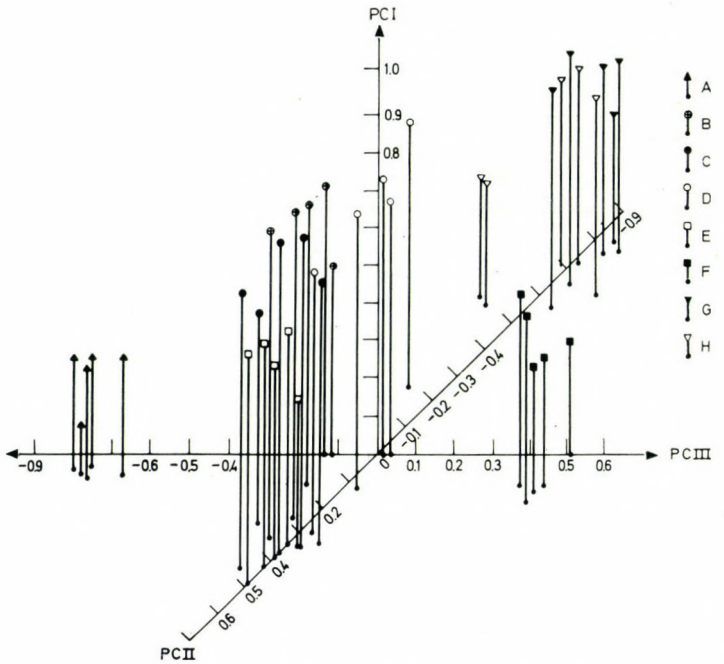

Fig. 17. Diagrammic representation of quadrats on the first 3 principal components axes

sional or seral axis (or else: a primariness-secondariness axis). In the middle (centre) the *Pulsatillo-Festucetum rupicolae* is found, close first of all to the noda from which it may be derived, and relatively also close to those which have been derived from it.

Instead of referring to the origin axis III can probably be brought into connection with the gradient of an abiotic factor ("hygrophily axis"), as *Calamagrostis epigeios* is rather a hygrofrequent, while *Chrysopogon gryllus* is a xerofrequent species.

As for the central position of *Pulsatillo-Festucetum rupicolae* we mention here that beside *PCA* the Euclidean distances also confirm it: the sum of distances from the other seven noda is the smallest in case of the steppe meadow:

Pulsatillo-Festucetum rupicolae = steppe meadow 16.5 ⟨⟨ *Danthonia-Festuca* type 20.6 ⟨ *Leontodon* type 22.5 ⟨

⟨ forest steppe meadow 24.2 ⟨ *Bothriochloa* type 26.8 ⟨ *Calamagrostis* type 28.1 ⟨

⟨ *Chrysopogon* type 30.1 ⟨⟨ *Agropyron* type 35.1

Discussion

It has long been known that the degradation process of swards and grasslands is characterized by a few species, including some *Poaceae* which become dominant. The appearance of dominant species indicates a certain point of the degradation series not only in the mountains but also in the analogous lowland xeroseries. Some dominance types (e.g. *Agropyron repens*, *Bothriochloa ischaemum*) are known to develop both in the progressive and degradative succession. There is not evidence however, as to how certain "preclimax" and "postclimax" stages are related to one another as regards composition. Very little is known about the composition of the developmental stages and their relations in the process of transformation. It is the dominants often sharply separated in space that suggest the discreteness (patchiness) of vegetation. It is to be noticed that a process in which one or more species become dominant reflects the response of the original vegetation (or of some elements of it) to perturbation at a lower level of degradation (in case of grasses: stimulation of polycormon formation). At the same time, the process of weeds overgrowing an area shows a different phenetic picture and does not by any means suggest "discreteness". A good example of invasion by a foreign element on the area studied is *Ononis spinosa;* originally it may have been a frequent species of mesophilous hayfields. It advances frontally with grazing irrespective of vegetation type: it is able to diffuse in any of them. On the other hand, the more closed and natural types of vegetation more or less resist to it. These two extreme examples side by side are rather contrasting; in any case they give opportunity to put the question of whether it is the changes of composition caused by degradation that produce such extreme dispersal responses, or it is the other way round: a change in the dispersal responses of populations (in other words: in the population dynamics) is responsible for the compositional changes.

According to the results of our investigations the separate stages are units that are not independent from one another as regards their species composition, and do not possess 'differential' (diagnostical) species, except the oldest forest steppe meadow. In addition, to the own species combination cover values of species differing with types are equally or even more important. The basic importance of cover is indicated not only by its role in the recognition of types, because it is also verified by the evaluation of results, namely, the results obtained on the basis of cover values are usually better interpretable than those based on binary data. After all, these experiences suggest that the change of cover should be regarded as responsible for subsequent changes of species composition.

The present paper analyses the dominance types and stages with a comparative view as if fixing them in time, and not in their process of develop-

ment. They are studied by categorization methods usually applied to dynamically unrelated phytosociological units. We can state that multivariate analyses were of great help in verifying and developing a traditional, empirically constructed hypothesis. The syndynamic relation is expressed in a similarity of composition, too. The agglomerative clustering methods, for example confirmed the close relation among the secondary grassland (*Danthonia-Festuca* type), forest steppe meadow and slope steppe grassland, and at the opposite end the closeness of the derived communities, the *Bothriochloa* and

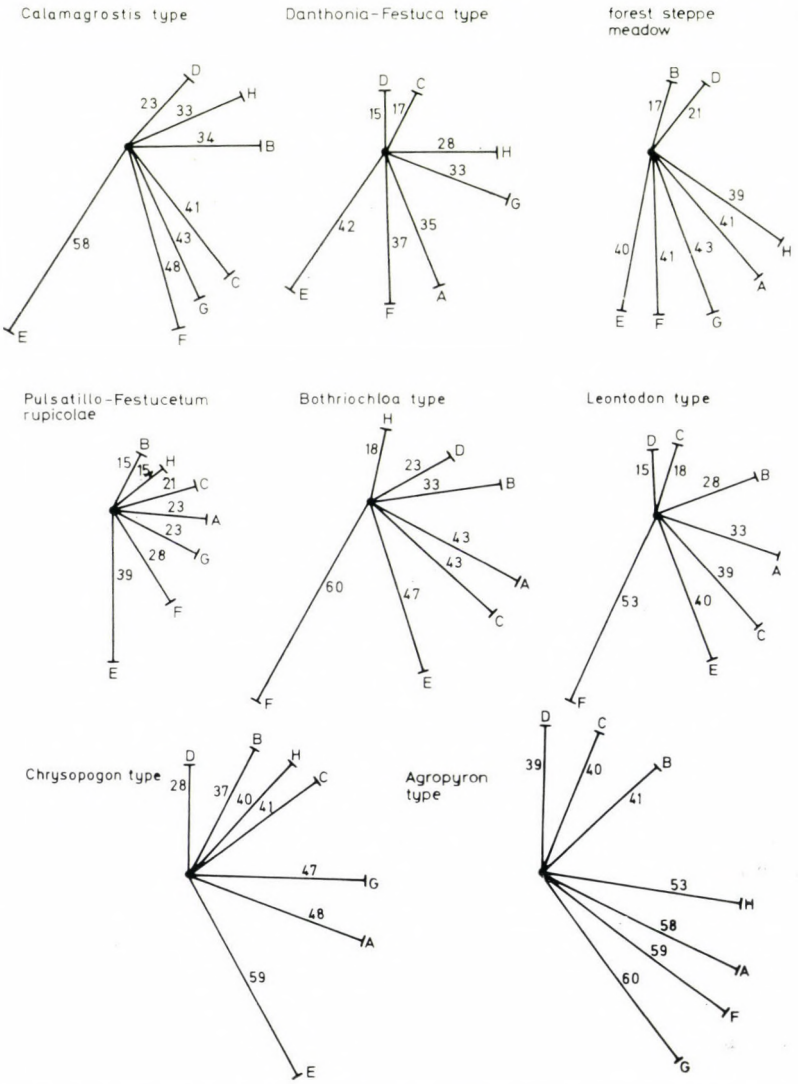

Fig. 18. Schematic illustration of Euclidean distances between vegetation types

Leontodon types. The picture obtained with *PCA* both verifies and enriches the views of derivation and convinces us of the discrete existence and separability of the stages.

Stages in which the average similarity (correlation) of the replicate plots was the highest, and the standard deviation (coefficient of variation) was the lowest were regarded as "coordinated". On this basis the most "coordinated" stages were the two derived vegetation types, the *Agropyron* and *Chrysopogon* stages. In the types at the two ends of the series (in the forest steppe meadow and the *Leontodon* stage) the average similarity of the replicate plots was low and the standard deviation was high. These types would be regarded as the least coordinated ones. At first sight it is surprising that the undoubtedly original forest steppe meadow is heterogeneous in its replicates. We must not, however, forget that the flora is the richest in this stage, though it is also true that the stands of the forest steppe meadow on the investigated area and in its neighbourhood are relicts of a previous climax community. Thus, as the migration processes have ceased or become difficult, the further species exchange of the stands is hardly ensured. The *Calamagrostis* and *Danthonia-Festuca* stages considered to be as earlier phases preceding the present subclimax are also heterogeneous, particularly the latter. The forest steppe meadow, the *Calamagrostis* and the *Danthonia-Festuca* types comprised also the most heterogeneous clusters. As regards coordination, and also in forming homogeneous clusters those two stages "excel" (*Agropyron*, *Chrysopogon*) where the extent of perturbation is moderate.

We may ask whether the full length of the degradation series is still "living", and how the relation between adjoining stages is interpretable. Representing the extent of relation between the stages in a diagram (Fig. 18) we find that the distance is the smallest between the *Pulsatillo-Festucetum* and *Danthonia-Festuca* types and also between *Pulsatillo-Festucetum* and the *Leontodon* types.

These similarities may suggest that two steps of the degradation series are still living even today. One is the impoverishment in species from the direction of the *Danthonia-Festuca* type towards the *Pulsatillo-Festucetum rupicolae*. The other is the degradation process that is from the *Pulsatillo-Festucetum rupicolae* towards the *Leontodon* stage as well as to some extent towards the *Bothriochloa* stage, mainly caused by selective grazing, trampling (soil erosion as a background process, series of species exchange: immigration of ephemeral species and ruderals).

The central role of *Pulsatillo-Festucetum* type has already been mentioned, this may serve as a "source" in the degradation process. In such a process certain derived types are separated from the steppe meadow to different extent (cf. the distances). It is the *Calamagrostis*, *Chrysopogon* and *Agropyron* types that are isolated to the greatest extent from each other and from all

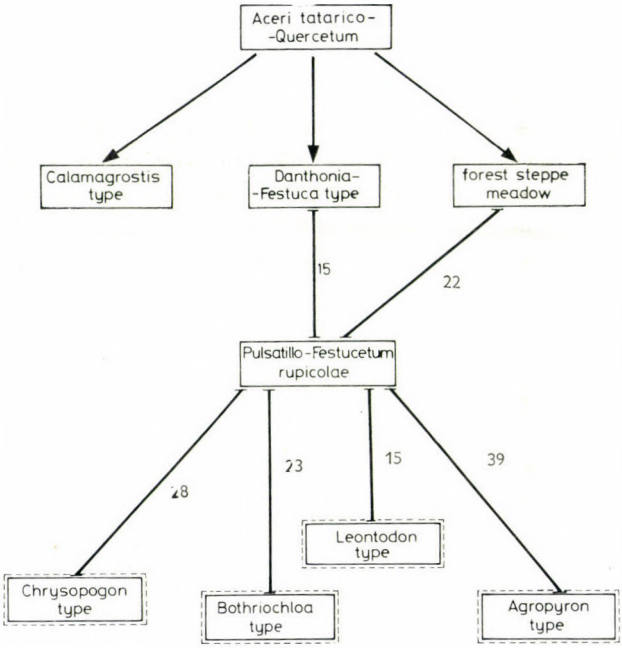

Fig. 19. Succession scheme

the other vegetation types. Regarding the two types, from which the *Pulsatillo-Festucetum rupicolae* would have been derived, at present the steppe meadow shows closer relation to the *Danthonia-Festuca* type than to the forest steppe meadow. In this interpretation the spatial separation reflects also an temporal change.

To show the one-dimensional distance of the units from one another we redrew Fig. 1 (Fig. 19).

Both this figure and the other analyses of composition allow for the following conclusion. The existence of clusters fused at various levels, the different Euclidean distances among vegetation types, the results of *PCA* ordination, the lesser or greater extent of discontinuity may suggest that degradation was not in the past, and is not at present an even process, but takes place by larger or smaller "leaps".

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PHENOL AND NON-STRUCTURAL CARBOHYDRATE CONTENTS IN THE LEAVES OF *QUERCUS PETRAEA**

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In this paper the changes in phenol and soluble carbohydrate contents in the leaves of groups of the *Quercus petraea* budding in different periods were investigated in 1981. One of our purposes was to describe the seasonal changes and the other was to compare the phenologically different groups. The connection between the quantities of these materials and the individual number of the phytophagous organisms were studied. The non-structural carbohydrates were determined by the antron-sulfuric method, the phenols by the FOLIN-DENIS test.

Besides describing the seasonal change a difference in the quantities of the soluble carbohydrates could be detected between the trees budding in various periods of time, while in case of the phenols only the seasonal dynamics could be registered. A rather demonstrative negative correlation could be observed between the individual number of the phytophagous organisms and the phenol content of leaves which indicates the number of the phytophagous organisms and the phenol content of leaves which indicates the important role of the phenols in bringing up a protection against external attacks.

Introduction

The conceptions on role of the secondary metabolic products have been modified considerably last time. These compounds can be used for exploring the phylogenetic connections, and they also play an important role in the defensive mechanisms of plants (LEVIN 1971). They can be investigated favourably as their chemical stability is generally high, and nowadays good analytical methods are known for detecting them.

Phenols and their derivatives are popular phytochemical markers, as they are to be found in the higher plants and their biosynthesis too, is more or less known. They can be easily transformed into glucoside form, become inactive, oxydized. Their specificity is based on the variability of these structures (SIEGELMAN 1964, ALSTON 1967). Recently the phenols get into the centre of attention ever frequently as the potential defensive compounds of plants (LEVIN 1971). They play an important role in bringing up the constitutive and induced resistance (WAHIMOTO 1958, VALENTA 1962, FARKAS 1962, BEN-AZIZ 1967). Many phenols belong to the group of the phytoalexins. The phytoalexins (MÜLLER 1956) are specific defensive compounds with small molecules, which are produced in plants under the influence of infection. The defensive reaction is limited to the neighbourhood of the infection. The basis of the resistance is the oxidation of the phenols into chinones (SEEVERS 1970).

Plants are capable, through their secondary metabolic products to reduce the attack of the consument and pathogen organisms. Species and individuals, with various defensive

* Síkfőkút Project, No. 83.

mechanisms have a selection advantage over the other plants and thus they can reach a higher reproductivity.

In our investigations the change of the phenol content and total soluble carbohydrate content in the leaves of the *Quercus petraea* was studied. On the one hand we tried to answer the question how the quantity of these organic compounds changes during the vegetation period, on the other hand, what the connection is like between these two groups of compounds to be easily transformed into each other. We wondered if there is any difference in the quantities of these compounds among the groups of trees budding in various periods, and of this difference has an effect on the various phytophaga injuries.

Material and method

Sampling

Samples were taken from the trees *Quercus petraea* in the area of Síkfőkút Project. 15 trees have been appointed and the trees were divided into three groups: early budding trees (E), trees budding at average time (A) and late budding trees (L). These phenological types can be well separated and are constant. The samples were taken monthly at the same time.

Chemical analyses

The collected leaves were drying, grinded and the chemical analyses were carried out with the thus prepared samples. The phenols were determined by the FOLIN-DENIS test (FOLIN 1927). The total soluble carbohydrate content (non-structural carbohydrates) was measured by the antron-sulfuric method, after an extraction with boiling water (BOURLEY 1980).

Results

Seasonal change of phenols

The values (Table 1) measured at the individuals were averaged regarding budding types and were shown in Fig. 1. In the early spring period there was a well observable difference between the late budding trees and these budding early and at average time. At this time a considerably higher phenol content was measured in the leaves of the late budding trees. During the vegetation period these differences are diminishing and the three tree

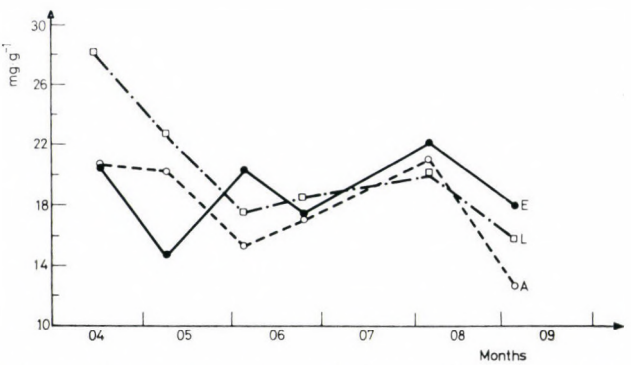

Fig. 1. Seasonal change of phenol content in the leaves of *Quercus petraea*. — E = Early budding trees; A = trees budding at average time; L = late budding trees

Table 1

Quantitative change of phenol content in the leaves of Quercus petraea
(mg/1 g dry matter)

Budding type	Sampling times					
	04 16	05 08	06 04	06 24	08 05	09 05
E_1	—	13.80	27.05	18.59	23.90	26.63
E_2	—	13.05	16.96	—	18.54	—
E_4	25.28	16.75	19.89	—	22.45	16.67
E_5	19.90	19.53	13.18	15.20	18.80	14.57
A_1	15.90	15.00	16.52	15.97	23.19	10.15
A_2	—	22.83	18.97	—	20.10	—
A_3	18.77	17.56	13.45	14.45	24.10	13.35
A_4	25.02	18.63	13.79	16.77	—	8.84
A_5	18.60	23.47	16.43	20.88	—	—
L_1	—	21.51	11.88	-20.02	16.29	15.62
L_2	22.10	22.90	18.30	20.03	14.44	—
L_3	39.21	22.45	23.32	—	30.03	—
L_5	22.78	24.14	16.95	15.25	—	—

E = Early budding trees; A = Trees budding at average time; L = Late budding trees

groups with different phenological type become similar. The spring decrease can be observed first in the early budding trees, thus the fact cannot be considered an accident that phytophaga damaged these trees first.

Seasonal change of the soluble carbohydrates

Values of the water soluble carbohydrates measured in the individuals (Table 2) were averaged regarding budding types (Fig. 2). During the vegetation period a continuous increase can be observed in the soluble carbohydrate content of leaves. In the spring period the group

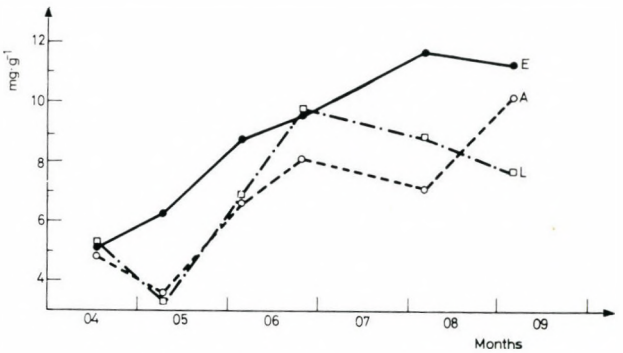

Fig. 2. Seasonal change of soluble carbohydrates in the leaves of *Quercus petraea*. — E = Early budding trees; A = trees budding at average time; L = late budding trees

Table 2

Quantitative change of soluble carbohydrates in the leaves of Quercus petraea
(mg/1 g dry matter)

Budding type	Times of sampling					
	04 16	05 08	06 04	06 24	08 05	09 05
E_1	—	4.71	7.27	6.52	9.37	12.49
E_2	—	4.70	11.41	—	15.57	—
E_4	5.29	5.37	7.59	—	10.45	11.33
E_5	4.91	10.41	9.16	12.80	11.63	10.23
A_1	4.72	4.30	6.56	7.09	8.51	7.78
A_2	—	3.65	4.59	—	7.02	—
A_3	4.91	2.98	8.63	9.52	5.99	10.56
A_4	4.95	3.97	4.81	6.48	—	12.28
A_5	4.98	2.73	8.73	9.52	—	—
L_1	—	3.61	6.88	6.66	6.38	7.52
L_2	4.76	2.06	5.02	12.87	4.87	—
L_3	5.83	2.88	8.16	—	15.60	—
L_5	4.70	4.91	7.52	9.87	—	—

E = Early budding trees; A = Trees budding at average time; L = Late budding trees.

Table 3

Two-factor variance-table for phenols

Factor	SQ	FG	MQ
Month (Factor A)	99.50	4	24.88*
Phenological type (Factor B)	15.54	2	7.77**
A×B	145.36	8	18.17*
Remain	93.86	15	6.26
Total	354.26	29	

* p = 5%, ** p = 10%.

of the early budding trees react differently, while in the summer period the trends of all the three types is different.

Changes can be explained on the one hand by the increase of the assimilating surface and on the other by an increased synthesis of the important compounds supplying and reserving energy. The increase is the steadiest in the early budding trees. The late budding trees, however, are similar but there is a considerable difference in the time intervals. It seems that the trees budding later recover the time lost by summer, by quickening their metabolic processes. The same could be observed in leaves of the young shoots developing simultaneously with the insect swarming (BÉRES 1981).

Table 4

Two-factor variance-table for soluble carbohydrates

Factor	SQ	FG	MQ
Month (Factor A)	85.84	4	21.46*
Phenological type (Factor B)	33.32	2	16.66*
A×B	36.09	8	4.51
Remain	69.33	15	4.62
Total	224.58	29	

* p = 5%.

Table 5

Correlation between the phenol content and soluble carbohydrate content, supposing a linear connection

Budding types	Correlation coefficient
E_1	0.7626
E_2	—0.9198
E_4	—0.2588
E_5	0.1766
A_1	—0.4367
A_2	—0.4869
A_3	—0.6275
A_4	—0.7265
A_5	—0.5613
L_1	—0.6820
L_2	—0.0429
L_3	0.1452
L_5	—0.9597

E = early, L = late budding trees; A = trees budding at average time.

Comparison between the changes of the phenol and carbohydrate contents

Two-factor variance-analysis was carried out to establish how the change of seasons and the individual budding types influence the quantities of phenols and carbohydrate during the vegetation period.

In case of phenols the quantitative change (Table 3) was influenced to a large extent by the seasonal variances and the different effects producing them (climatic effect, state of development of the plant, physiological effect etc.). The individual budding types differed

to a lesser extent (there was no significant interaction on a level p = 10%, either). However, when the combined effect of the two factors was studied, a difference could be observed among the three types. But this arises not from the differences among the three groups but from the seasonal differences in phenol content.

In case of soluble carbohydrate content both factors (months and budding types) have an effect on the quantitative changes (Table 4). Consequently, the groups of trees budding at different times can be markedly separated from this point of view.

Studying the connection between the carbohydrates and the phenol-content (supposing a linear connection as a first approach) the trees budding at average time differed from the other two groups (Table 5). A moderately strong negative correlation was obtained. It seems that the negative correlation between the two groups of compounds presented itself most normally in these trees.

Connection between the number of phytophaga and the quantities of investigated compounds

We ended the quantitative investigations by studying the question if the phenol and carbohydrate contents of the leaves of the *Quercus petraea* have a regulating effect on the individual number of the phytophagous organisms consuming them (Table 6) the data of

Table 6

Correlation between the phenol and soluble carbohydrate contents and the individual number of the phytophagous organisms

Time of sampling		Budding type		
		E	A	S
04 16	F	20.59	20.37	28.02
	Sz	5.10	4.89	5.10
	Σ	98.52	128.68	77.44
	P	27.60—	17.44	17.44
05 08	F	14.65	20.44	22.50
	Sz	6.25	3.73	3.37
	Σ	54.05	98.48	58.49
	P	19.88	47.26	18.33
06 24	F	17.28	16.86	18.43
	Sz	9.66	8.15	9.80
	Σ	620.94	394.89	362.95
	P	319.88	280.29	362.95
08 05	F	22.02	21.00	20.25
	Sz	11.76	7.17	8.95
	Σ	405.39	425.91	474.97
	P	64.10	166.34	129.28

F = Average phenol content (mg g^{-1}), Sz = average carbohydrate content (mg g^{-1}), Σ = number of all the phytophaga organisms (on 1000 leaves), P = number of phytophagous organisms (on 1000 leaves) (data of L. SZABÓ), E = early budding trees, A = trees budding at average time, L = late budding trees.

four points of time have been summed up and compared with the number of the phytophagous organisms to be found then on the same trees (the results of L. SZABÓ). Relying on the table it can be stated that the defensive role of the phenols seems to be proved in our case as well, as in each case the fewest phytophaga could be found on the trees the phenol content of which was the highest.

We could not find a positive correlation between the sugar content and Aphids moreover we observed a distinctly negative correlation here, too.

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BOOK REVIEWS

Editor: G. FEKETE

CZIMBER, GY.: A kerti zsázsa (The Garden Cress). Magyarország Kultúrflórája 7.7 (Kultúrflóra 51) Akadémiai Kiadó, Budapest 1982

The cultivation and production of the cruciferous plant species having been naturalized in Europa in the age of the Romans and used widely for both nourishment and as a medicinal plant has almost entirely ceased in Hungary in our days. Hence, it is no accident that a detailed description of this undeservedly neglected cultivated plant has just been presented to the general public and agricultural experts by a ten-man research group led by the Author. All the knowledge gathered on this species in the literature and by means of Hungarian and foreign research c rried out in our days has been compiled in 14 chapters provided with a contents written in Hungarian, English and Russian languages.

In the first three chapters an outline of the onomasiology of the species, its taxonomic place, relationship and origin as well as its distribution and cultivation history, are given making use of numerous related works. Its primary source of origin is Abyssinia, while the secondary centre of origin of the wild ancestors is twofold: that of the spinescens subspecies in Abyssinia, Egypt and Syria while that of the silvestris variety extends from East-Africa to Southern-West Asia. Its utilization in European countries dates back to ancient times; mainly in the eastern countries a considerable amount is used even today as salads, groceries, a medicinal plant, and from its seeds oil is pressed as well. Lots of data relating to its cultivation in Hungary can be found and in spite of the fact that 9 t seeds were produced to be exported in 1965, today its organized production has been ceased in Hungary. It can be found in regions of the country only growing wild from the older cultures or possibly in private cultivation. The next two chapters deal with the external and internal morphology of the plant in the order of the individual organs. The morphological differences between the two most frequently produced varieties (those of segmented leaves and those of entire intact ones) and the results of the manifold ¡morphometric comparative investigations carried out on these are described in detail. The differences between the individual organs of the two varieties are shown even better in the excellent histological sectional drawings, which illustrate the chapter including the internal morphology of the garden cress. The next three chapters describe the ontogenesis of the plant, from germination to full development of the flower and fruit. From this physiological approach newer features of the species are revealed thus e.g. the extremely rapid germination; in 6 hours after the soaking the radicle appears and in already 20 hours' time the whole absorption zone of the root forms itself. The comparative germinative experiment carried out with mustard-seed also led to a surprising result. From the data of the phenological photograph it turns out that in two weeks the rosette develops to a size which can already be used as a salad, then within three months counting from sowing the plant ripens to a fruit. Comprehensive observations were made to compare the developments of the stands grown by glasshouse and field technologies, relating to the segmented and entire varieties and differences in the photosynthetic systems which have been proved by the many kinds of indexes of the growth analysis. In the further part the ecological characteristics, parasites and cultivation technologies of the species are detailed. It should be noted that the plant has a soil exacting feature and is suitable as an after-seed for indicating the radioactive isotopes in the treated soils. A detailed description is given of the possible ways of cultivation, and the necessary macro- and micro-element demands of the soil. The author discusses the reasons why this plant has not been cultivated in Hungary. Furthermore the possible modes of utilization of this plant which has a high vitamin C content

and which could be produced at low coasts especially as winter salad, the basal leaves and young stem leaves of which could be used as species due to their special aroma. Its leaves have been used with good results for different exanthemata in folk therapy and are excellent for expelling water. It can be used extremely well for biotesting due to its sensitiveness to herbicides. The last chapter describes the forms of the species, the possibilities for improvement and the culture varieties used in production at present.

This comprehensive elaboration can be recommended not only to agricultural and horticultural experts but it can also serve as a useful reading for teachers lecturing biology at any level. Besides it may be useful in the better utilization of the weekend garden-plots, where the experimental cultivation of various kinds of vegetables and greens may be carried out.

Z. KERESZTY

KINZEL, H.: Pflanzenökologie und Mineralstoffwechsel. Verlag Eugen ULMER, Stuttgart 1982, 534 pp., 178 figures, 96 tables

Besides Prof. KINZEL, H. other well-known authorities, such as ALBERT, R., ERNST, W. H. O., HOHENESTER, A., KUSEL-FETZMANN, E.–WEBER, M. also took part in writing the individual chapters of this book.

In the book comprising eight chapters the mutual effect of the habitat conditions and the soil and plant, the connection of the environment with the mineral metabolism are described. These interconnections determine the occurrence of the natural vegetation and a knowledge of these is very important for the agriculture, too.

Chapter 1. In the Preface KINZEL, H. emphasizes that all phenomena of plant ecology are closely connected with physiology. It is a task of the ecophysiology to determine the habitat factors and the adjustment of the plants to these.

Chapter 2. In this introductory chapter KINZEL, H. describes such questions as for example the physiologic, ecologic character of the plants and their determination on the basis of the chemical composition and ioncontents. The formation of ecotypes and the importance of the competition are discussed and a survey is given of the problems and objects of the ecologic research.

Chapter 3. A detailed description is given (ALBERT, R.) of the ionintake of the halophytons and the chemical composition of the species living in different natural habitats. Several investigations have been carried out with different salt concentrations, in connection with the growth and development of the plants. As the salt-contents of the water used for irrigation is a limiting factor for agriculture in semisalt-affected acid areas, the investigations related to the salt-tolerance of the cultivated plants are very important. The changes in production, osmosis and intake of nutrients with different salt concentrations (NaCl) and the toxic effect of salt have been investigated.

Different types of plants living in alkali soil can be separated on the basis of the ioncomposition. The notion "physiotype" is used, which can be applied to concrete taxons (species, population, family). The physiotype excells among other taxons in its special physiological constitution (specific features of mineral metabolism). The mechanism of saltregulation can be measured in the whole plant organism. Such adjustment forms are succulence and salt-selection. On a cellular level the salt has an effect on the enzymes, hormone balance, photosynthesis and on the formation of the carbohydrate and nitrogen.

On the basis of their dispersal, the plants can be divided into the following groups: obligate halophytons, facultative halophytons and halophytons and glycophytons living in different habitats.

As a supplement of this chapter, a survey is given of the salty alkali soils, their formation and spread, by HOHENESTER, A.

Chapter 4. The calcicole, calcifuge, basiphil and acidophil plants are described in the chapter by KINZEL, H. As it can also be seen from the related literature, the chemical reaction and lime content of the soil, as a factor depending on the climatic zone and defining the difference in the vegetation, is very important mainly in Central and Western Europe. A survey is given of the causal connection between the pH value of the soil and the nutriment intake of the plants. The notions of the calciphob, calciotroph and acidophil, basiphil, calcifuge and calcicole plants, respectively, are determined physiologically and ecologically. The calcic intake, metabolism, calcic absence and calcic profusion are dealt with in detail.

The species of the individual families (e.g. *Poaceae*, *Cyperaceae*, *Juncaceae*) behave relatively uniformly towards the Ca. Their ion-content is less dependent on the chemical composition of the environment. The calcium has an effect on the enzymes and is a measure

of enzyme activity. The calcium absorption of the roots and the calcium transportation into the parbs above the ground differ with the calcifuge and calcicole species.

The potassium, magnesium, nitrogen and phosphorus contents of the soils also have an effect on the calcium intake of the plants.

Calcium has an effect on the nitrifying dynamic processes taking place in the soil and on the nitrate-reductase activity.

The concentration of the aluminium-ions in the soil depends on the acidity of the soil, this element is toxic for lots of plants. Iron, manganese, copper, zinc, molybdenum and boron can also be found in toxic concentrations. The chemical effect of the soil plays an important role in the formation of the Mn, Fe and Al contents of the plants. The hydrogen-carbonate to be found in the water-balance of the soil impedes the iron-intake, while facilitating the ammonium-intake.

The author describes lime-chlorosis to be observed in the soil rich in $CaCO_3$, mainly in vine-cultures, some species of the *Fabaceae* family and some species of fruit trees (apple-tree, peach-tree).

In Chapter 5 the serpentine plants are described (KINZEL, H.–WEBER, M.). That soil is called serpentine, which can be found in several places of the Earth and cannot be defined petrographically, where in the toxic heavy metals, especially nickel and chrome can be found in relatively large quantities. Due to the presence of heavy metals and magnesium in toxic quantities plants of specific physiognomy occur. The nutrient contents of the plants is very low. The physiological features enabling plants to live in serpentine-soils also are described.

In Chapter 6 the plants of boggy soils are included (KUSEL-FETZMANN, E.). A description of the features of the peat soils is given, the quantitative relations of the fungi, bacteria and animals (Collembolas, Nematodas, Acari) playing an important role in decomposing the organic matter, the distribution of the humus materials, the mineral contents of the peat and boggy water as well. Nitrogen and phosphorus are found in small amounts.

The main constituents of the peat-bogs are the peat mosses, the water absorption of which can be 26 times larger than their dry weight (*Sphagnum palustre*). Due to the low pH value and the reduction relations the toxic metal ions, such as Mn, Zn, Pb and Al are to be found in relatively large quantities in the peat.

In Chapter 7 the heavy metal plants are included (ERNST, W. H. O.). There are several elements among the heavy metals, such as Fe, Mn, Zn, Cu, Co, Mo, which are indispensable for the plants. Ni and V have a restricted physiological importance. The following elements have no physiological importance: Cd, As, U, Pb, Th, Cr, Hg, Ag. A survey is given of the so-called heavy metal soils, their chemism and of the ecophysiological relations of the heavy metal plants. The heavy metal tolerance of plants is also described.

A detailed bibliography including the recent results of research follows each chapter of the book. The work, based on a wide range of the research results, has met a great need, and is intended to fill up the gap which has existed between the purely ecological and purely physiological approaches.

This book may prove to be invaluable for botanists, ecologists, physiologists and agricultural experts.

M. KOVÁCS

GEORGHIOU, G. P., SAITO, T. (eds): Pest Resistance to Pesticides. Plenum Press, New York 1983, 805 pp.

During the past decade, resistance to pesticides among pest species has increased to the point where it is now considered to be the most serious obstacle to effective pest control. Since house flies first developed resistance to DDT in 1946, more than 428 species of arthropods, at least 91 species of plant pathogens, 5 species of noxious weeds and two species of nematodes were reported to have developed strains resistant to one or more pesticides.

A seminar of U.S.A. and Japanese scientists was held in Palm Springs, California, U.S.A., during December 3–7, 1979, under title "Seminar on Pest Resistance to Pesticides: Challenges and Prospects", in order to evaluate the status of research on resistance and to discuss directions for future emphasis. A total of 32 papers were presented under three principal topics: Origins and Dynamics of Resistance (6), Mechanisms of Resistance (18), and Suppression and Management of Resistance (8). The Seminar was unique in that it brought together for the first time researchers from the disciplines of entomology, plant pathology and weed science for a comprehensive discussion of this common problem. This book contains all the 32 papers.

Out of these papers one may see significant advances mainly on the subsequent four fields:

a) the development of methods for detection and monitoring of resistance in arthropods (electrophoresis, diagnostical dosage tests) and plant pathogens,

b) research on biochemical and physiological mechanisms of resistance (cytochrome P^{450}, sensitivity of target site, gene regulation),

c) the identification and quantification of biotic, genetic and operational factors influencing the evolution of resistance, and

d) the exploration of pest management approaches incorporating resistance-delaying measures.

The content of the book falls into three sections.

I. Origins and Dynamics of Resistance

Historical, genetical, methodological and modelling aspects of resistance and its detection, monitoring and evolution.

One of the papers deals with the resistance of plant pathogens to chemicals introduced in the past decades. Comprehensive lists are given on chemicals to which no resistance has been detected, for which resistance in plant pathogens has been detected in laboratory tests but not in the field, and to which resistance has been detected under field use. Detailed elaboration also given for a resistance detection or monitoring program for general use, including standard methods for sample collection from field, and laboratory tests. There is a general evaluation of the most commonly used fungicides (in USA) on the basis of the number of fungicide-resistant pathogens on the given chemical. In fact it is the list of failures in disease control. The biggest failure is connected with benzimidazoles where 81 plant pathogens were detected in USA, to be resistant.

II. Mechanisms of Resistance

Some important topics of this section: Role of oxidases, hydrolases, esterases, and reduced sensitivity of the nervous system in insecticide resistance; patterns of cross-resistance; the kdr factor; penetration, binding and target insensitivity.

An extensive study of herbicide resistance of higher plants is also given. Some natural weed population have developed spontaneously a partial or complete resistance to one or more herbicides but in every cases it occurred in the field after cca. ten years of successive treatment with the same chemical. Resistant strains of several crops (*Zea mays*, *Daucus carota*, *Nicotiana tabacum*) have been laboratory selected and developed through cell culture. Several herbicide binding model have been worked out for explanation of resistance on biochemical level.

The mechanisms of fungicide resistance with special reference to organophosphorus fungicides were studied intensively in the last decade. The most probable mechanisms of resistance to a fungicide are: Modification at the site of action of the fungicide, decreased permeability of the fungal cell membrane to the fungicide, and altered metabolism of the fungicide within the fungal cells. Fungal metabolism of organophosphorus thiolate (PTL) and related fungicides was reviewed in relation to resistance to the fungicides in strains of *Pyricularia oryzae* of various sensitivities. In one of the moderately resistant isolates from the fields, the increased detoxification by cleavage of the thiolate bond was seemingly a resistance mechanism to the PTL fungicide IBP.

Green and blue mold of citrus fruits are incited by the widespread fungi *Penicillium digitatum* Sacc. and *P. italicum* Wehm. Since 1940, several mutants of them have been reported with stable resistance to biphenyl and other similar fungicides. These resistant mutants are present at low frequencies in the natural population of *Penicillium* species in citrus groves, but under the selection pressure created by postharvest fungicide treatments, these strains may become the dominant components of the population in packinghouses. The recommended management strategy against these fungicide-R strains also discussed.

III. Suppression and management of resistance

The alternative possibilities of suppression are: suppression through chemical structure modification, by combination of synergistic pesticides, and at the case of fungicide resistance, by a special sequence of fungicides that is unfavourable to the buildup the resistant strains.

As for plant pathogens, in the past many pesticides have not been as subject to resistance in pests as insecticides. This is because most plant disease control chemicals have been multisite inhibitors, whereas most of the modern insecticides and acaricides were relatively selective biochemically. After the introduction of site-selective compounds for plant desease control, especially fungicides, numerous cases of resistance occurred.

A variety of pesticides, ideally both site- and non-site-specific, will be necessary to deal with resistance, and the development of new structures with a wide variety of biochemical

actions should be encouraged. However, the regulatory and economic climate throughout the world is not conductive to such development of new pesticides.

What role resistance will play in plant disease control in the future is unknown, but it certainly will be a significant deterrent to the promiscuous use of many limited-side pesticides. Resistance has altered markedly the thinking of those designing chemical control programs for plant diseases, although there is considerable diversity of opinions as to how to prevent resistance. Much more research is needed on resistance before plant pathologists can develop and prove more effective strategies to deal with this disturbing aspect of crop production.

This highly informative volume will be very useful for every professional researcher of pest resistance to pesticides.

Z. Szőcs

N. E. WEST (ed.): Temperate Deserts and Semi-deserts. Ecosystems of the World 5. Elsevier Publ. Co., Amsterdam 1983, 522 pp.

As a part of a series edited by D. W. GOODALL, this volume meets a long-standing need of a comprehensive, up-to-date description of temperate deserts and semi-deserts. The task of writing and editing such a review must have been extremely difficult since the information on temperate semi-deserts has previously been scattered among a vast, sometimes inaccessible, number of journals published in many languages. Despite this problem, the editor and contributors were capable of bringing together all materials available that concern the structure and functioning of terrestrial ecosystems found under dry, temperate climates.

Temperate deserts and semi-deserts are restricted to Eurasia and North and South America; they decrease in extent in that order. This unequal distribution determined the primary structure of the book. There are three main sections in addition to an introductory and closing section, each consisting of a single chapter. Section II (Chapters 2 through 10) describes the continental, semi-desert ecosystems of Eurasia, including those of the Caspian Lowland, Kazakhstan, Middle Asia, Central Asia, the Pamir Mts, Afghanistan, and Iran. The next section (Chapters 11 through 16) discusses the North American semi-deserts that are distributed along the high mountains in the west. The only chapter of Section IV is devoted to the relatively small semi-desert area in Patagonia.

Because of differences among approaches applied to the particular areas, the structure within chapters of the book is not uniform. For example, detailed autecological, production biology and geobotanical surveys are reported from the USSR, whereas incomparably more emphasis is laid on land-use and ecosystem functioning in the North American contributions. As a result, comparison of continents is difficult, if not impossible, in several aspects. As Prof. WEST himself points out in the last section, there is still a strong need for an integrated ecological research in the semi-desert areas of the world to diminish these differences.

There is no doubt that this book, being a pioneer summarization of existing results, is an indispensable source of information and an encouraging collection of research topics for all ecologists interested in desert research. The presentation is attractive and numerous black and white photographs, as well as even more line drawings and tables, are included in the text. It is a pity that individuals can hardly afford the price of this book; thus, it is a must for libaries, especially in the countries concerned. Certainly, we are looking forward to the remaining volumes of this series to appear.

J. PODANI

FELSENSTEIN, J. (ed.): Numerical Taxonomy. SPRINGER Verlag, Berlin–Heidelberg–New York–Tokyo 1983, 644 pp.

This volume is not a textbook, as one might expect looking at the title, but a collection of papers presented at a numerical taxonomy meeting held in Bad Windsheim, West Germany, in 1982. As such, the quality of contributions is unbalanced, so much the more because the editor purposely avoided suggesting any significant change in the manuscripts by saying that the ". . . papers are as the authors wanted them to be". However, this variability is an advantage indeed, as one not fortunate enough to be present at the conference may be able to appreciate the stimulating scientific atmosphere of the proceedings. The only thing one has missed was the wine-tasting experiment associated with M. B. LIMA's presentation on the classification of Portuguese wines.

Fortunately, the book is not an incomprehensible mass of unarranged material. J. FELSENSTEIN did a good job by ordering the papers such that the reader interested only in

philosophical or methodological problems does not have to go through all the abstracts, summaries or conclusions. However, some structuring of the book was necessary as the number of articles was about seventy, much more than in any other previous proceedings on the subject of numerical taxonomy.

The first set of papers demonstrates the controversy over phenetic and cladistic approaches to classification. Many arguments and interpretations of results are given in several attempts to convince the reader about the superiority of a particular approach. This reminds me of the old ecological issue of whether clustering or ordination techniques should be preferred in revealing structural relationships among vegetational entities. This problem does not exist any more in plant ecology as both methodologies have been simultaneously used for more than a decade. I agree with J. McNeill in that numerical taxonomy has a similar future and possibly in ten years some synthesis of cladistic and phenetic techniques will be accepted as being the most fruitful method of analyzing taxonomic relationships.

The papers of the second section treat the problem of taxonomic congruence. R. Sokal, F. J. Rohlf et al. and K. Fiala provide comparisons between phenetic and cladistic classifications. Other contributions are concerned with prediction, consensus methods and distributions of indices for tree comparisons. This section overlaps with the next in which interest is focussed upon multivariate techniques. J. C. Gower discusses various criteria for comparing classifications, D. W. Matula's study deals with the problem of cluster validity. Additional topics discussed in this section are the significance of clusters, evaluation of clusterings and matrix comparisons.

The reconstruction of phylogenetic relationships is the topic of the next section. D. H. Colless reviews some problems of constructing Wagner trees while G. F. Estabrock, W. Le Quesne and C. A. Meacham analyse character compatibility. The editor of this volume elaborates on a statistical view of methods for inferring phylogenies. Papers on analyzing morphological and geographical variation comprise the next two sections followed by applications of numerical taxonomic methods to various fields of biology, such as biochemistry, ecology, genetics and behavioral studies. The last four papers deal with the use of computers in systematics. Of these, the one expressing Felsenstein's personal views on the future of computerized taxonomy is really worth reading.

In summary, the book gives valuable information on the current state-of-the-art of numerical taxonomy. It should be present on the bookshelf of and, what is more important, it should be consulted by anyone dealing with either theoretical or applied aspects of the subject.

J. Podani

Dunn, G. and Everitt, B. S.: An Introduction to Mathematical Taxonomy. Cambridge Studies in Mathematical Biology 5. Cambridge University Press 1982, 152 pp.

In agreement with the title, this book has been written at an introductory level for biologists and others interested in the application of numerical methods to taxonomic problems. Consequently, it has not claimed to be a competitor of the more comprehensive, although older, texts such as Sokal and Sneath's Numerical Taxonomy or Everitt's Cluster Analysis. The clear structure of the book makes it very readable. Numerous examples are included to illustrate the usefulness of the numerical approach in analyzing taxonomic relationships. Although written for beginners, even those familiar with the techniques presented may find the book useful in selecting the appropriate method. One is warned, however, that some knowledge of matrix algebra and basic statistics is necessary to understand the principles of most multivariate techniques. Thus, this book may still prove difficult to follow at some places for "pure" biologists.

The first subjects discussed are the philosophy and aims of numerical taxonomy. Some views of traditional and numerical taxonomy are contrasted with the conclusion that neither approach is superior to the other (numerical taxonomists usually agree . . .). After the introduction the selection of characters, character coding and weights are described. Although the text is deliberately incomprehensive in several aspects, the various scale types could have been treated at some length in this chapter (only the internal scale is mentioned). Some selected resemblance coefficients are discussed next. The authors' judgement is sound, the functions listed are the most widely used ones in practice (perhaps Jaccard's index is an exception). Principal components analysis, whose knowledge is prerequisite to other ordination techniques, is illustrated with simple examples in Chapter 4. Various techniques of multidimensional scaling and cluster analysis have received the most attention (Chapters 5–6). Just like the resemblance functions, the multivariate procedures selected for discussion have

been standard methods of numerical taxonomy. There is a chapter on identification and assignment in which discriminant analysis and canonical variate analysis are introduced, among others. The authors' preference to phenetics is obvious as the topic of evolutionary trees is restricted to a single and short chapter at the end of the book. Another comment is that some information on the available computer program packages could have been given in a separate Appendix.

Once again, this book is recommended as an introduction. As such, it should not escape the attention of every potential user of mathematical methods. Be careful when ordering, however, since the cover is a bit overvalued by the publisher (softbound at £5.95 vs. hardbound at £15.00), indicating a trend not really welcome by libraries.

J. PODANI

TRYON, R. M. and TRYON, A. F. (eds): Ferns and Allied Plants with Special Reference to Tropical America. Springer Verlag, Berlin 1982, 857 pp.

The volume is a detailed analysis of the pteridophyte flora of North and Central America giving thorough descriptions of 29 families and 3000 species of 127 genera. The horse-tails (*Equisetopsida*), lycopods (*Lycopsida*) and water-ferns (*Marsileineae, Salviniineae*) are also covered besides ferns (*Filicopsida*). The tropical species are of course the most particulary treated, some less important genera which are not native to the tropics are discussed in less detail.

In the Introduction the authors outline their classification system to be used in the book. This system essentially differs from other previously used systems (CHRISTENSEN, COPELAND, HOLTTUM, CRABBE, PICHI-SERMOLLI) demonstrating that pteridophyte taxonomy is still subject to considerable changes. There are few fixed points of reference in this field and further changes can be expected until an approximately realistic picture reflecting the evolution of pteridophytes is obtained. The difference from previous classifications is due to the introduction of several taxa suggested based on new SEM-studies and phytochemical data.

The biogeographical part of the Introduction gives a brief overview on the range of American species, the centers rich in species, different habitats and important occurrences of endemics. Of the 3250 American species cca. 3000 are found in the tropical zone of the continent where especially the montane regions are diverse and rich in fern species. Four regions in the tropics have outstanding significance. These regions are remarkable for the great number of endemic species and the richness in species.

In the following part the authors stress the significance of spores which have received an increased attention since the introduction of modern techniques making detailed examinations possible. This provides new data to reveal evolutionary trends and processes, and the relationships among taxa. In the cytological section basic chromosome numbers of the genera of families covered in the volume are found and several cytological aspects of chromosome numbers are discussed. At the end of the Introduction an identification key to the families of American ferns is given. The keys to genera and species are placed after the characterization of each family. The Introduction ends with the references.

In accordance with the arrangement of the material first we get a survey of the families followed by lower level taxa, such as subfamilies, genera and species. As a preliminary to each family full morphological characterizations are given covering all parts of the fern: prothallium, differentiation of stems and sporogenesis. The synonyms are also listed here. The next section comprises the theoretical problems of pteridophyte taxonomy and analyzes the relationships and evolutionary states of families. The authors draw a parallel between fossil and recent species. In many cases fossil specimens prove to form a link between certain recent species or genera.

In the biogeography section we get a picture about the distribution of families and species with emphasis on the endemics. This is followed by the cytological characterizations of families. These sections are all illustrated with photographs of the highest quality. Photographs taken in the habitat of each species, detail-drawings clearing up the diagnostic characters and microphotos make the description complete and unambigouos. In this way nearly all characters of the important species can be seen on photos. Details of leaves, venation, vegetative and fertile stems, the main periods of sporogenesis, and rhizome and epidermis appendages are all well illustrated by the close-up photos. In order to emphasize essential features, the photos are supplemented with sciagrams and detail-drawings.

The characterization of each family is followed by a key to the American genera. Using this key we get to the next chapter, the description of genera. The characterization starts with a full list of generic synonyms followed by a detailed morphological genus descrip-

tion similar to that of the family characterization. This is completed with distribution maps summarizing data from the six largest American herbaria and institutes. Then, the subgenera, their taxonomical relations and descriptions are presented including data on the number of species and species groups included in each genus.

The ecological section deals with the description of habitats and plant communities. This is followed by a summary of geographical data and the discussion of endemics developed as a consequence of geographical isolation. The most interesting chapter is probably the one about spores. After the description of spore surface morphology, amazing SEM-photos are seen which show the finest details of spore surface. The curiosity of pictures of $\times 1000$ magnification is intensified by photos of $\times 10\,000$ magnification. The pictures were usually taken from different views on the some species facilitating precise identification based on the fine structure of spores. The spore photos of related species are found next to one another so their comparison is easier.

Looking at the figures of this volume it becomes obvious that the microworld of spores is as diverse as the fronds which bring the spores into existence.

In the cytological part the chromosome numbers of the species of each genus are collected. Having the basic numbers and combinations the relationships among species can be examined and conclusions can be drawn regarding and perhaps we can poliploidy level and hybridization. The absence of chromosome numbers for some tropical species shows the difficulty with certain critical genera. This section is closed by a bibliography of the relevant literature. The volume including 3000 taxa is one of the most important handbooks for the experts of pteridophyte taxonomy and palynology, and may also be recommended for anybody else interestes in this field of botany.

T. SZERDAHELYI

HESS, H. D.: Die Blüte. Eine Einführung in Struktur und Funktion, Ökologie und Evolution der Blüten (The Flower. Introduction to the Structure, Function, Ecology and Evolution of the Flower). Verlag Eugen Ulmer, Stuttgart 1983, 428 pp.

The two most widely-spread hobbies in Europe are tourism and home-gardening. In the German Federal Republic 70 per cent of the population declare themselves as lover of gardening. Although usefulness has become the main aspect, a garden is not a garden without flowers. When on an excursion the beauty and harmony of the vegetation restore our lost balance. Plants now form an integral part of the modern home and are decorative elements of more and more working places; still we hardly know their life, and many of us do not even know their names. It is not by chance that the claim of incorporating the knowledge of plants in the general culture arises from many sides. The number of those amateurs engaged in raising and propagating plants while having the opportunity of acquiring a thorough knowledge of their interesting world is ever increasing. This book that focusses on the flower as the most interesting plant organ has also been written to promote this activity. Besides describing the structure and function of flowers it shows their close connection with the surroundings and tells the history of their evolution in an easy style. The reader is encouraged not only to collect pieces of information but also to verify them. This purpose is served by the easy tasks of observation or examination given at the end of each major section. The author makes his explanations vivid by his own photos; his main endeavour was to show the inner, seldom seen parts of some flowers in high magnification. The didactic value of the book is founded on the readily appreciable multicolour drawings which help the understanding of processes and relationships. For the sake of easy handling the text is printed in two columns. Pleasing and economical is the fashionable form of placing most of the drawings and captions on the margin by the text.

In the first chapter, after a short description of the structure of flower, a brief survey of the taxonomy and nomenclature is given. Then, the 20 major families of Angiosperms are characterized according to flower structure. The most characteristic forms and the major varieties within the family are listed. In addition, the formulae of the typical chemical substances and the structural elements of the flower are shown in figures. The form of flower most characteristic of a family is illustrated in a colour plate. The most important facts established so far about the flowers are discussed in 10 subsequent chapters grouping the subjects by biological aspects.

The second chapter deals with the conditions and ways of plant reproduction starting from the cell whose functioning and substances are evaluated from the point of view of reproduction. After describing the evolution of all cryptogamous phyla the author analyses the life cycles of the Angiosperms while making the reader gradually acquainted with the most

important genetic conceptions and phenomena. This thorough and extremely suggestive discussion of the cryptogamous groups exceeds the topic indicated by the title, yet, the author is excused by his endeavour to represent the evolution of plants and of the flower within.

In the following chapters the physiology of pollination is treated with the organic and inorganic factors taking part in it. The alluring behaviour of the flower is shown by the author as the manifestation of a kind of sexual instinct. In this context he gives a detailed analysis of the shape, colour, odour and sexual stability of the flower and describes the conduct and role of animals taking part in the process of pollination. Interesting information is given on the sense of colour of animals, the relation between the physiological clocks of plants and animals, and on the UV studies of flower colours. According to the way and physiology of pollination the flowers are placed in categories and subcategories, with the best known species listed for each. After that the author sets up groups according to the pollinator animals. Then the prevention of self-pollination is dealt with. Dioecism and asynchronous maturing, development of organs of different shape and position, self-sterility and incompatibility are considered from this point of view: then self pollination and concealed pollination, homozygosis and heterosis are discussed. In chapter 10 a brief survey is given of tissue cultures, vegetative hybridization and of the most recent results of gene transplantation.

In the last chapter the phylogenesis of various flower structures from the Triassic to these days is outlined. The parallel phylogenesis of the different flower types and their insect pollinators is represented in a figure (p. 397). The origin of species, the possibilities and problems of natural hybridization, the relationship between ecological niche and phenological isolation are dealt with in detail.

The work is completed by detailed lists of references and subjects; the latter includes the scientific names of species without the authors, as usual in popular works. The concepts and species names found in the descriptions of methods are given in a glossary.

Being a popular work in the first place the book tries to give full explanation of all phenomena, and may therefore seem sometimes too lengthy or too sketchy for professionals. In spite of this, it serves the purpose, although not intended to impart high level knowledge. What it says wins the reader's liking, and this is a viewpoint not to be neglected! As a special merit of the book, the aspects of evolution are constantly emphasized, important relationships disclosed, and botany is made an integral part of the living world. That is why we sometimes feel as if the enormous bulk of material even in abstract form burst the frames of the individual subjects. By discussing the flowers the author has carried out, in fact, an outlined summarization of the whole botanical science of today, according to the most up-to-date viewpoints and in a didactically excellent grouping. The book is therefore specially recommended to thos studying biology and botany at universities, to secondary school teachers, and to all communities dealing with plants in the form of self-education groups or study circles. Teachers and leaders of study circles can use it as a manual, as it contains an examination material elaborated and grouped by subjects. The book with its rich content and nice get-up is an eloquent testimony of how much is still hidden waiting for discovery in the world of plants.

Z. KERESZTY

ETTL, H.: Chlorophyta I. Phytomonadina, in: ETTL, H., GERLOFF, J., HEYNIG, H., MOLLENHAUER, D. (eds): Süßwasserflora von Mitteleuropa (Freshwater flora of Central Europe). Vol. 9. G. FISCHER Verlag, Jena 1983, 807 pp.

The series "Süsswasserflora von Mitteleuropa" (Freshwater flora of Central Europe) has become richer with a new volume. The author is the internationally best known expert of the subject, who has written some excellent monographs, e.g. on *Chloromonas* and *Chlamydomonas*, published in 1970 and 1975, respectively.

After the preface and the list contents a taxonomic key to 13 classes of algae, from the *Cyanophyceae* to the *Cryptophyceae*, is found.

The first chapter of the book gives a characterization of the phylum *Chlorophyta*. Within the morphological structure the monadoid, capsalis, coccalis, trichalis, siphonalis stages of organization are described. In discussing the reproduction of green algae, division, reproduction with zoospores, hemiautospores, autospores, copulation, iso-, aniso- and oogamy are presented. Information is given on the resting stage, and on the distribution and occurrence of green algae. The division of the phylum into 7 classes and 29 orders is based on the most recent taxonomic results.

The second chapter contains a general description of *Phytomonadinae* and a detailed treatment of the orders, genera and species.

In the general part the reader is acquainted with the cell structure, morphology, reproduction, resting stage, distribution and ecology of *Phytomonadinae*. Detailed information is given on study methods, *Phytomonadina* cultures, microscopic studies and identification. The phylum *Phytomonadinae* is divided into 3 classes and 5 orders:

Prasinophyceae		
Polyblepharidales	13 genera	59 species
Halosphaerales		
Tetraselmidales	2 genera	10 species
Chlorophyceae		
Dunaliellales	17 genera	48 species
Chlamidophyceae		
Chlamidomonadales	48 genera	880 species
Volvocales	13 genera	40 species

After the general description the above classes and orders are discussed in detail. For each class a general characterization is provided. The genera of a particular class, order or family are illustrated by a characteristic species. Taxonomic keys to the orders, families and genera within each class are presented. For *Chlamydomonas*, the most populous genus, even sub-genus keys are given. Within each genus the taxonomic keys to species are found. The taxonomic keys are based on light microscopic morphology. The work is completed by a detailed description and one or two, or sometimes even three, drawings of each species. After discussing the species of a genus the author lists the sea- und salt water species, and the uncertain taxa.

At the end of the book a bibliography (478 items) and a subject index are found. The 1120 figures represent, in fact, 3000 drawings of algae.

Due to the simple, clear structure of ETTL's work with its detailed morphological treatment, precise description of species and large number of drawings the identification book can be used by anybody in the profession with great confidence. Apart from the algologists, the excellent work is warmly recommended to systematists, hydrobiologists, and other biologists working in the practice of water management. In addition, the book is suitable for use in university education and in all fields where the knowledge and exact identification of *Phytomonadiane* are important.

K. T. KISS

HÄUSLER, J.: Schizomycetes, Bakterien. Süßwasserflora von Mitteleuropa. Band 20. VEB Gustav FISCHER Verlag, Jena 1982, 588 pp., 340 figures

The identification book of aquatic bacteria of Central Europe edited by H. ETTL, J. GERLOFF and H. HEYNIG represents a part of the planned 24-volume series launched by A. PASCHER.

The book falls into a general part followed by ten chapters, a bibliography and a subject index. The first chapter deals with the phototrophic bacteria supplemented with those living in "consortiums". Chapter 2 discusses two orders of sliding organisms. The next chapter summarizes the regularly sheathed gram-negative bacteria. Chapter 4 presents the organisms reproduced by abscisic spores and decorated with various forms of flagellae and other appendages. The author emphasizes the artificial character of this group as no evolutionary relationships exist among the taxa. Twenty-one genera are listed, including *Planctomyces* which is of particular interest for us: some of its species are often very abundant in the waters of Hungary (Lake Balaton, Danube, fishponds, etc.(. The fusion of *Planctomyces crassus* with *P. Békefii* seems arguable since they usually occur together, e.g., in the Danube, and no intermediate forms are observed regarding the thickness of arms. Unfortunately, only a few Hungarian authors are referenced, although a relevant paper (Acta Microbiol. Acad. Sci. Hung. 27, 259–268) just published in 1980 should have deserved attention. Our standpoint is expressed in two publications in preparation (HAJDU and HORTOBÁGYI).

Chapter 5 deals with the Spirochaetes. Four genera from the family of *Spirochaetaceae*, and two other from the *Leptospiraceae* are discussed. Several doubtful and inadequately described species of *Spirochaeta* are mentioned. The sixth chapter deals with the coiled and wavy bacteria assigned to two families, *Spirillaceae* and *Spirosomaceae*. This chapter also contains many taxa with uncertain taxonomic position. Chapter 7 summarizes the spherical and rodlike gram-negative aerobic bacteria. The eighth chapter is devoted to the chemolithotroph sulphur bacteria. Only one family, *Thiobacteriaceae*, is mentioned. Chapter 9 deals

with the chemolithotroph iron- and manganese-accumulating organisms. Genera and species with doubtful taxonomic position are also found here. The title of the tenth chapter is Addendum. According to our present knowledge, the genera included are very difficult if not impossible to assign properly to any of the above discussed categories. Their number is twelve. Some incompletely described species, doubtful genus assignments and very little studied orders are also discussed in this chapter. The 55-page bibliography has to be also mentioned, although the respected author ignores most results published in Hungary. Only five authors (BOKOR, GIMESI, HAJDU, HORTOBÁGYI and SCHERFFEL), one papers by each, are cited. Regrettably, the others have escaped the author's attention. The number of items in the bibliography is still 1348 altogether!

It is a fine and very useful book recommended for bacteriologists, hydrobiologists, algologists, university and highschool teachers and any others interested. Being a pioneer work, the book has some unavoidable but negligible drawbacks. The subject is difficult, anyway, and a synthesis like this needs a wide knowledge for appropriate judgment. The presentation of the book is admirable, the nice figures show essential characters.

T. HORTOBÁGYI

MISAGHI, I. J.: Physiology and Biochemistry of Plant-Pathogen Interactions. Plenum Press, New York and London 1982, 287 pp. + XVI

This excellent book brings together the literature on the biochemistry and physiology of plant parasite interactions. It is an up-to-date reference to the current state of pathophysiology of plants. Thus, advanced students, researchers and teachers of the biochemistry of healthy and infected plant can use it successfully. The recent results accumulated in the seventies and eighties are included into the text but some important early literature is also mentioned. Treating the subject, the author begins with the penetration and infection processes, then discusses the pathogen produced metabolites and the alterations in plant structure and function. Emphasis has been made on the recognition process between plant and pathogen (surface-surface interaction between the two organisms).

Chapter 1 deals with the definitions (symptoms, pathogenicity, virulence, tolerance, compatibility, hypersensitivity, biotrophs, etc.). The subsequent chapters are dealing with penetration of pathogens, the role of cell-wall-degrading enzymes, toxins, altered permeability, water relations in diseased plants, pathological carbohydrate metabolism, alterations in transcription and translation, phenol metabolism, growth regulators, physiology of tumors, mechanism of disease resistance, induced resistance and specificity of host-parasite interactions. At the end of the book some useful books are recommended for further studies. There is an extremely useful and modern collection of references and a subject index in the book.

The text is readable. The knowledges are very well summarized and the author pointed out several uncertainties whenever it was possible and necessary.

This fine summary is highly recommended for those who are working in the fields of plant pathology, plant physiology, biochemistry and plant breeding.

Z. KIRÁLY

WOOD, R. K. S. (ed.): Active Defense Mechanisms in Plants. Plenum Press, New York and London 1982, 381 pp. + X p.

This is the 37th volume of the NATO Advanced Study Institutes Series and contains the papers presented at the symposium held in Cape Sounion, Grece, 21 April–3 May, 1981. Sixteen lectures were held and all of the participants read contributed papers. Only the summary of the contributed papers are published in this volume, in addition to the whole texts of the lectures. The discussions are not included in the book. All of the papers are dealing with those defence mechanisms that follow changes in the host caused by the pathogen. The passive mechanisms that are independent of the pathogen, are not included in the text.

The book begins with an account on the general aspects of active defence mechanisms (HEITEFUSS). The subsequent lectures deal with the structural view of active defence (INGRAM), physiological and biochemical events associated with expression of resistance to disease (BAILEY), mechanisms conferring specific recognition in gene-for-gene plant-parasite systems (KEEN), determinants of plant response to bacterial infection (SEQUEIRA), defence mechanisms of plants against varietal non-specific pathogens (TOUZÉ and ESOUERRÉ-TUGAYÉ), mechanisms in non-host resistance (MATTA), the absence of active defence mechanisms in compatible

host-pathogen interactions (HEATH), plant immunization-mechanisms and practical implications (KUC), genetical aspects of active defence (ELLINGBOE), active resistance of plants to viruses (HARRISON), localized resistance and barrier substance (LOEBENSTEIN, SPEIGEL and GERA), the protective effects of systemic virus infection (FULTON), regulation of changes in proteins and enzymes associated with active defence against virus infection ((VAN LOON), antiviral agents and inducers of virus resistance: analogies with interferon (GIANINAZZI), the effect of defence reactions on the energy balance and yield of resistant plants (SMEDEGAARD-PETERSEN).

The book is extremely useful for researchers in the fields of plant pathology, genetics, plant breeding and plant physiology. At the end of the book the subject index helps the reader to find quickly themes, definitions and pathogens. The editor has done a perfect work in arranging the texts of the lectures and contributions. This volume will be a valuable piece of a series of books recently published on plant pathophysiology and disease resistance.

Z. KIRÁLY

ASADA, Y., BUSHNELL, W. R., OUCHI, S. and VANCE, C. P.: Plant Infection: The Physiological and Biochemical Basis. Japan Scientific Soc. Press, Tokyo and SPRINGER Verlag, Berlin, Heidelberg and New York 1982, 362 pp. + XVIII

This symposium volume contains the proceedings of a U.S.–Japan meeting held May 17–22, 1981 in Brainerd, Minnesota on the physiological basis of plant infection and to commemorate the contributions of two internationally known Japanese professors, K. TOMIYAMA and I. URITANI. The book covers the recent findings of broad areas of disease physiology: penetration, the hypersensitive reaction, the role of phytoalexins and preformed compounds in disease resistance, specificity of host-pathogen interactions, toxins, metabolic alterations in diseased plants, induced resistance and induced susceptibility, the development of symptoms in infected plants.

Y. ASADA summarized the recent advances in Japan in the physiology of plant infection. The subsequent papers and discussions are dealing with the sites of action of disease determinants (DURBIN), initial events during penetration (SHERWOOD and VANCE), primary germ tubes of powdery mildew conidia (KUNOH), infections by *Rhizobium* (BAUER), elicitation and suppression of the hypersensitive reaction (DOKE, TOMIYAMA and FURUICHI), hypersensitivity in rusts and powdery mildews (BUSHNELL), physiology of induced susceptibility (OUCHI and OKU), immunization of plants against virus, fungus and bacterial diseases (KUĆ), metabolic alterations in response to wounding and infection (OBA et al.), metabolic regulation in plant pathogens (KOSUGE and COMAI), mitochondrial DNA associated with cytoplasmic male sterility and disease susceptibility (KEMBLE na PRING), host specific toxin of *Alternaria alternata* (NISHIMURA et al.), the host specific toxins of *Helminthosprium* spp. (DALY), chemical basis of host recognition by *Alternaria* spp. (UENO et al.), action sites for AM-toxin (KOHMOTO et al.), biochemical mechanism of glyceollin accumulation in soybean (YOSHIKAWA and MASAGO), phytoalexins (KEEN), phytoalexins as preformed antifungal substances (TANI and MAYAMA), detoxification of phytoalexins (VANETTEN), hypersentitive cell death (TOMIYAMA), biochemical approaches to general principles in plants underlying plant disease phenomena.

This symposium volume is highly recommended to those who are working on the fields of plant pathology, plant biochemistry and physiology and plant breeding.

Z. KIRÁLY

ACTA PHYTOPATHOLOGICA

ACADEMIAE SCIENTIARUM HUNGARICAE

EDITED BY

Z. KIRÁLY

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Borhidi, A., Muñiz, O., Del Risco, E. 1979*a*: Clasificación fitocenologica de la vegetación de Cuba. Acta Bot. Hung. **25**: 263–301.

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